PRINCIPLES
OF
BOTANY

BERGEN AND DAVIS

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March 23, 1908.

Attractiveness for insects in showy involucres of *Cornus canadensis*

After Conway MacMillan

PRINCIPLES OF BOTANY

BY

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PREFACE

The present work owes its existence to the favorable reception accorded to Bergen's *Foundations of Botany.* Whatever betterments have been suggested by five years' use of the earlier book in the hands of expert teachers will be found here incorporated. The *Principles of Botany* also attempts to supply what many feel to be one of the most valuable portions of botany for educational purposes, namely, a consecutive series of studies of representative spore plants, so treated as to outline the evolutionary history of the plant world. Botanical technology cannot figure largely in any brief general botany. The authors have however touched frequently upon the economic side of the subject, and the last two chapters are wholly devoted to practical topics.

The subject-matter has been divided into three parts, treating respectively:

I. The structure and physiology of seed plants (Bergen).

II. The morphology, evolution, and classification of plants, being an account of the critical morphology of plants upon which is based their relationship by descent (Davis).

III. Ecology and economic botany (Bergen).

The whole will furnish material for a full year's work, and it will usually be found necessary to omit portions and thus shape a course adapted for the exact conditions under which the work in each case is to be done. It is not the intention of the authors to frame an inflexible course, but rather to present in orderly fashion the material from which a thoroughly practical one can be planned. Indeed, the authors believe that a half-year course can be readily arranged by selections from the more general sections of the book.

The planning of a course will be materially assisted by the use of the authors' *Laboratory and Field Manual,* which is so arranged as to offer a choice between the general requirements of a shorter, elementary course and the details which are only possible when more time can be given to the subject, under excellent conditions of laboratory equipment and with fairly mature students. A glossary of botanical terms employed in this book will be found in the Laboratory Manual.

Some instructors will prefer to devote most of the year to a study of seed plants; others will choose to make the story of plant evolution the chief feature and may even prefer to begin with Part II. This portion of the book is the outgrowth of ten years' experience of the junior author in the University of Chicago, where he offered a year's course in general morphology along somewhat similar lines. The treatment given to the thallophytes in Part II will seem to some readers long in proportion to that allotted to the other groups of plants. This cannot however be avoided in any account which attempts to present an outline of plant evolution with the important topics of the origin and evolution of sex and of the sporophyte. Furthermore, it is very desirable to describe a range of types from which selections may be made according to the material available in different regions of the country. The adaptation of the book to several methods of approach has obviously necessitated slight repetitions of fundamental matter in certain parts.

Whatever the order of treatment, the authors would urge the importance of sending the student to the plants for as many as may be of his facts and then linking these together by reading and class discussion. Undigested laboratory work is little better than none at all, while a reading course without type studies and physiological experiments is a quarter of a century behind the best practice of to-day. No matter where it is to end, the study of botany should begin with a first-hand knowledge of plants themselves, — best of all, with a knowledge of their life in their own natural environment. At the outset there may be far more botany and more reasoning power gained in finding out for one's self the light relations of locust or bean leaves, or in ascertaining why one pool is teeming with *Spirogyra* and another with *Oscillatoria*, than in much reading of botanical literature.

The earlier chapters of Part I are considerably less difficult than most of the later portions of the book. It is therefore suggested that care should be exercised not to consume too much time in covering this ground, together with the laboratory work which it presupposes. Classes should rather be carried along somewhat rapidly to such more difficult topics as are discussed in Chapters V, VIII, XII, and XV, and in Part II.

Except where acknowledgment is made in the text, the figures and plates are all new or from the *Foundations* or *Elements of Botany* of the senior author. Most of the illustrations of Part II are original and by Dr. Davis. Special thanks for photographs and plates either reproduced in half tone or redrawn for zinc etchings are due to F. W. Atkinson, F. Börgesen, F. E. Clements, E. M. Freeman, G. L. Goodale, and Conway MacMillan. W. M. Davis, A. E. Frye, and F. Roth have kindly permitted the use of a number of woodcuts and maps.

Parts of the manuscript were read by A. T. Bell, F. E. Clements, I. S. Cutter, W. F. Ganong, R. A. Harper, W. M. Hays, J. C. Jensen, Miss Lillian J. MacRae, and Miss Caroline E. Stringer. Proof was read by W. J. Beal, F. E. Clements, W. N. Clute, I. S. Cutter, H. S. Pepoon, B. M. Stigall, and Miss Eva O. Sullivan. To all of these the authors wish to express their great appreciation for kindly criticisms and most helpful suggestions.

J. Y. B.
B. M. D.

CAMBRIDGE, August, 1906

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INTRODUCTION

Botany is the science which treats of plants. It considers the structure and functions of individuals, recognizes their neighborhood relations as citizens of plant communities, and studies their positions as members of the plant kingdom more or less closely related by common descent. The study of the individual plant embraces a variety of topics, and the examination of its relation to others introduces many more subjects.

Morphology is the science of form and structure. Under this head are studied the forms of plant bodies and the portions of which they are composed. All plants except the very simplest are made up of parts, called *organs*, which are structures developed for particular kinds of work. Thus the stems, roots, and leaves are organs, and so are also the parts of a flower. Morphology establishes the relationships of organs which seem at first glance very dissimilar, as when leaves take the form of bud scales or spines or tendrils. Morphology traces the degeneration of parts which frequently cease to perform the work for which they were originally developed and become much simplified in structure or almost disappear. Thus the tendrils of the woodbine are shown to be morphologically branches reduced to mere organs of attachment. Although morphology deals with the plant with less regard to its character as a living being, it should never be entirely separated from physiology, but should go hand in hand with that sister subject, equally necessary to an understanding of plant life.

Plant physiology treats of the plant in action, how it lives, respires, feeds, grows, and produces others like itself. It discusses the nature of the material in which the life activities of the plant have their origin, and the conditions as regards light, heat, air, and moisture under which life is possible. It considers the raw materials out of which plant food is made, the processes by which the manufacture is carried on, and the means by which food once produced is transported throughout the plant body. The mode of growth of plants is an extended and most important topic, and the processes by which reproduction is carried on are so numerous and complicated that they constitute one of the most difficult and interesting departments of botany. In order to go far into the details of the life activities of plants one needs to know a good deal of chemistry and some physics. But there are many of the phenomena of plant physiology which can be taken up with profit in an elementary way and investigated with rather simple apparatus.

Plant geography discusses the distribution of the various kinds of plants over the earth's surface.

Paleobotany, usually studied along with geology, considers the history of plant life on the earth from the appearance of the first plants until the present time.

Taxonomy, or systematic botany, is concerned with the classification of plants. By this is meant the arrangement or grouping of the kinds of plants to show their relationships to one another. It attempts to express the final results of the long processes of plant evolution, and is far more than the conventional study of flowering plants, which occupy only the highest grades in the elaborate system of plant evolution and classification.

Plant ecology treats of the relations of the plant to the conditions under which it lives, together with the origin and development of plant associations. Under this division of the science are studied the effects of soil, climate, and friendly or hostile animals and plants on the external form, the internal structure, and the habits of plants. The main lesson to be learned from the study of ecology is that the plant is not an organism of fixed form, structure, and habits, sprung from a long line of precisely similar ancestors and destined to leave an indefinite series of forms like itself to succeed each other in the same area. On the other hand, each generation is a little more or less numerous than its predecessors, covering more or less territory than they did, and varying from them this way or that under the influence of changing conditions of life. This is an interesting department of botany, but it has to be studied mainly out of doors.

Economic botany is the study of the uses of plants to man.

Many of the topics suggested in the above outline cannot be studied in detail in an elementary course. It ought, however, to be possible for the student to learn a good deal about the simpler facts of morphology and of plant physiology. It is necessary to study plants themselves, to take them to pieces and to make out the connection of their parts, to examine with the microscope small portions of the exterior surface and thin slices of all the variously built *tissues* of which the plant consists. Among the lower plants there will be found a most attractive study of cell structure, reproductive processes, and life histories, — all requiring the use of the compound microscope. Living plants must be watched in order to ascertain what kinds of food they take, what kinds of waste substances they excrete, how and where their growth takes place and what circumstances favor it, how they move, and indeed to get as complete an idea as possible of what has been called the behavior of plants.

Since the most familiar plants spring from seeds, the beginner in botany may well examine at the outset the structure of a few familiar seeds, then sprout them, and watch the growth of the seedlings which spring from them. Afterwards he can study in a few examples the organs, structure, and functions of seed plants, trace their life history, and so, step by step, follow the process by which a new crop of seeds at last results from the growth and development of such a seed as that with which he began.

After he has come to know in a general way about the structure and physiology of seed plants, the student may become acquainted with some typical spore plants. This will open up a new world, illustrating some of the most interesting and fundamental principles of biological science; for an understanding of the cell theory of organization and development, the nature of sexual processes, and the evolution of the plant kingdom with its remarkable alternation of generations, can only be gained by tracing the chief steps in the processes through the various groups of algæ, fungi, liverworts, mosses, and ferns.

For users of the book who wish to begin in the autumn with the study of some seed plant as a whole the following scheme is suggested:

1. Examine a seed plant in flower, to get an idea of its gross anatomy. Then study the development, structure, and modes of dissemination of the fruit. Outline the structure of seeds and follow the germination of some types. Next take up the structure and physiology of the vegetative members of the plant body, root, stem, and leaf.

2. Cover as much as may be of Part II, working out the story of the evolution of plants.

3. Devote the remainder of the year to study of floral structures, field work on families of angiosperms, ecological topics, and an outline of economic botany.

If desired, the course in botany may begin with the simplest spore plants, tracing the evolution of the plant kingdom through a consecutive study of types, as described in Part II, followed by somewhat detailed work on the structure and physiology of seed plants (Part I), and ecology (Part III).

Part I

THE STRUCTURE AND PHYSIOLOGY OF SEED PLANTS

CHAPTER I

THE SEED AND ITS GERMINATION

The seed. A seed is a miniature plant, or *embryo,* with some accessory parts, in a resting or dormant state, and capable under suitable conditions of reproducing the kind of plant which bore it.

The power of producing seeds is peculiar to the higher plants (seed plants, or *spermatophytes*) and sharply distinguishes them from all lower forms of plant life.

The embryo may nearly or quite fill the interior of the seed, as in Fig. 1, or it may constitute only a small part of the bulk of the latter, as in Figs. 3, 4.

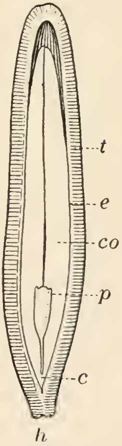

FIG. 1. Lengthwise section of a squash seed

c, hypocotyl; *co*, cotyledon; *e*, endosperm; *h*, hilum; *p*, plumule; *t*, testa. Magnified about two and a half times

2. Form and position of the embryo. The embryo shows great diversity of form; it may have one, two, or several seed leaves, or cotyledons (Figs. 1, 3, 12). These may be straight, as in the squash seed, or much curved and folded, as in the seed of the four-o'clock, morning-glory, or buckwheat, but they are almost always closely packed for economy of space.

The cotyledons are usually borne on a little stem, called the *hypocotyl* (meaning beneath the cotyledon) (Fig. 1, *c*; Fig. 2, *c*). Often a little seed bud, or *plumule* (Fig. 3), is easily recognizable in the embryo, more or less inclosed by the cotyledons, if there are two of these.

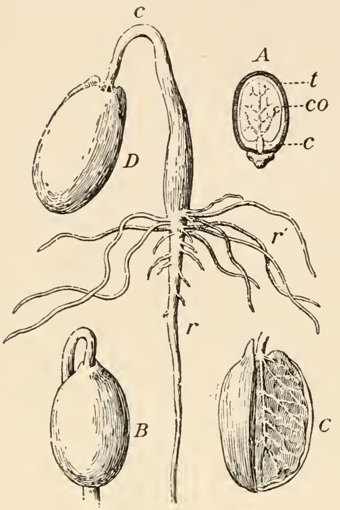

Fig. 2. The castor bean and its germination

A, lengthwise section of ripe seed: *t*, testa; *co*, cotyledon; *c*, hypocotyl. *B*, sprouting seed covered with endosperm. *C*, same, with half of endosperm removed. *D*, seedling: *r*, primary root; *r′*, secondary roots; *c*, arch of hypocotyl

3. The seed coats. The embryo (and sometimes other seed contents) is inclosed by one or more seed coats, which in many cases preserve the embryo from injuries of various kinds, and also serve other purposes. The principal seed coat is called the *testa;* it varies greatly in thickness, hardness, color, and markings, and also in other respects, as is evident when one recalls the varied appearance of such familiar seeds as those of the mustard, squash, bean, pea, locust, apple, poppy, and Brazil nut.

4. Topics for investigation. The student should learn at first hand (that is, from the seeds and the young seedlings themselves), in connection with the present chapter, something about the following topics:

1. The anatomy of a few typical seeds.
2. Some of the conditions for germination.
3. Some of the chemical changes produced in germinating seeds, and their effect upon the surrounding air.
4. The early steps in the development of seeds into plants.

The brief outline of the structure of the seed just given should be much enlarged by the details learned in the laboratory.

Every observing person who has grown plants from the seed has learned that heat and moisture are necessary to insure germination, but the student will readily discover, too, that air is necessary for anything more than the beginning of germination.

5. Oxidation involved in germination. Germinating seeds, like all living things, consume much *oxygen,* — the gas everywhere present in the atmosphere which supports the combustion of coal and other fires and of lamps and gas flames. In place of the oxygen which they absorb, sprouting seeds return to the air *carbon dioxide,* — the gas which is produced by burning charcoal, and which is one of the products of burning most kinds of fuel and of the respiration of animals.

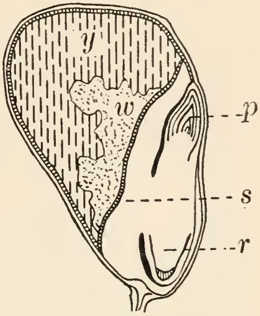

Fig. 3. Lengthwise section of grain of corn

y, yellow, proteid part of endosperm; *w*, white, starchy part of endosperm; *p*, plumule; *s*, the shield (cotyledon), in contact with the endosperm for absorption of food from it; *r*, the primary root. Magnified about three times. — After Sachs

A thermometer with its bulb immersed in a jar of sprouting peas will mark a temperature somewhat higher than that of the room in which they stand. The elevation of temperature is at least partly due to the union of oxygen with combustible materials in the peas. Such a combination is known as *oxidation.* This kind of chemical change is universal in plants and animals while they are in an active condition, and the energy which they manifest in their growth and movements is as directly the result of the oxidation going on inside them as the energy of a steam engine is the result of the burning of coal or other fuel under its boiler. In the sprouting seed, much of the energy produced by the action of oxygen upon oxidizable portions of its contents is expended in producing growth, but some of this energy is wasted by being transformed into heat which escapes into the surrounding soil. It is this escaping heat which is detected by the thermometer.

CHAPTER II

THE STORAGE OF FOOD IN THE SEED

6. Importance of stored food for growth of the seedling. A very large part of the food of man and of many of the higher animals consists of seeds of various kinds, particularly of the grains. Every kind of seed contains some stored food material, though the amount in the poppy seed is but an insignificant fraction of that in a horse-chestnut. Very often, as has already been learned, the food is stored directly in the embryo, especially in the cotyledons. Frequently, however, most of it is deposited in the *endosperm,* which surrounds or lies alongside of the cotyledons (Figs. 2, 3, 4). In either case the slow germination and subsequent growth of seeds from which part or all of the food material has been removed shows that its presence is most important in forcing along the growth of the seedling (Fig. 5).

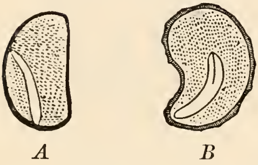

FIG. 4. Seeds with endosperm, longitudinal sections

A, asparagus (magnified); *B*, poppy (magnified). — After Decaisne

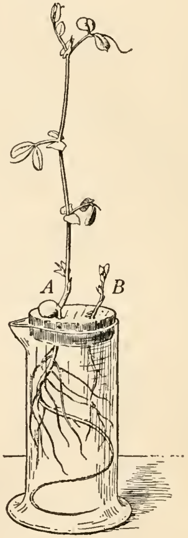

FIG. 5. Germinating peas, growing in water, one deprived of its cotyledons

7. Usefulness of rapid growth of seedlings. The very existence of the young plant may depend upon its being able to make a rapid start in life. Most areas of fertile land contain far more seeds than can mature plants under the conditions of competition with one another which they must encounter, and so plants which shoot up rapidly at first possess a decided advantage. There is also a much better chance for seedlings growing in woodlands if they can attain considerable size before they are too much shaded by the foliage of the trees above them. This, of course, does not apply to evergreen woods.

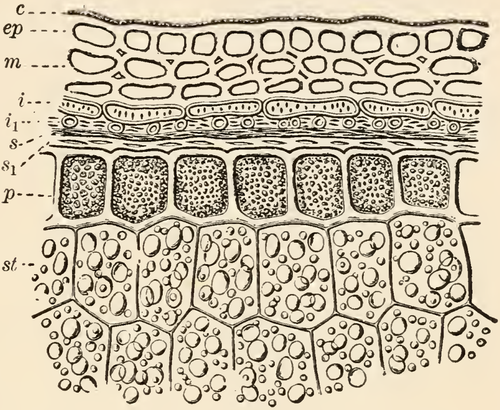

FIG. 6. Section through exterior part of a grain of wheat

c, cuticle, or outer layer of bran; *ep*, epidermis; *m*, middle layer; *i*, i_1, layers of hull next to seed coats; *s*, s_1, seed coats; *p*, layer containing proteid grains; *st*, cells of the endosperm filled with starch. Greatly magnified. — After Tschirch

8. Kinds of food stored in seeds. The three principal kinds of plant food, or reserve material stored in seeds, are starch, oil, and albuminous substances, or *proteids*.[1] A single seed may contain all three of these in considerable proportions, or it may contain proteids together with either starch or oil. Some proteids are always present, since the power of the seed to live and grow depends upon these compounds.

9. Starch. Every one is familiar with the appearance of starch in its commercial form. As found in seeds it occurs in microscopic compartments known as *cells* (Fig. 6). Each cell contains many small starch grains, usually of a nearly round or an ovoid

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[1] As in general throughout the book, the statements of the text presuppose a suitable amount of laboratory work; for example, that of the manual of the authors.

shape. The shape and markings of a starch grain, whether found in the seed or in some other part of the plant, are often sufficiently definite to serve to identify the kind of plant from which they came. Frequently the markings are very regular and beautiful, as in canna starch (Fig. 7). They are due to the successive layers deposited as the starch grain is formed. During the growth of the seedling, seeds containing starch rapidly lose it, and microscopical examination of a sprouting grain of corn or of the cotyledons of a bean plant several weeks old shows the cells comparatively emptied of starch and those grains which remain much eaten away, as described below.

Fig. 7. Canna starch
Magnified 300 diameters

10. Action of ferments. A substance which can produce or excite any one of the chemical changes known as fermentation is called a *ferment.* The most familiar kinds of fermentation are the *alcoholic,* by which alcohol is produced, and the *acid,* by which solutions of alcohol (such as fermented cider) are turned into vinegar, and by which the sugar of milk is changed into lactic acid when sweet milk turns sour.

All these fermentations and many others are caused by the development within the fermenting substances of minute living organisms, either *yeasts* or *bacteria,* described in Chapter XXII, which are consequently known as *organized ferments.*

There is a class of substances which, without the presence of yeasts or bacteria, can produce active fermentation. From the absence of the organisms above-mentioned, these are called *unorganized ferments,* and they are also known as *enzymes.* One of these, *diastase,* plays a most important part in seeds during germination, transforming starch into sugar. Diastase is found in considerable quantities in malt, which is barley sprouted and then quickly killed by moderate heating. Naturally, as a result of the action of its diastase, malt tastes much sweeter than barley. The capacity of this enzyme to change starch to sugar is extraordinary, any quantity of diastase sufficing to transform ten thousand times its weight of starch.

11. Oil. Oil occurs in many seeds — as, for example, flax, cotton seed, and corn — in sufficient quantity to make it worth while to extract it by pressure. It may be seen under the microscope in extremely minute droplets, inclosed in the cells of certain regions of the seed.

12. Proteids. Sometimes, as in Fig. 6, at *p*, the proteid constituents of the seed occur in more or less regular grains, but often they have no well-defined form and size. They have a chemical composition very similar to that of white of egg or the curd of milk, and when scorched produce the familiar smell of burnt hair or feathers, which serves as a rough test for their presence.

13. Other constituents of seeds. Besides starch, oil, and proteids, other substances occur in different seeds. Some of these are of use in feeding the seedling, others are of value in protecting the seed itself from being eaten by animals or in rendering it less liable to decay. In such seeds as that of the nutmeg, the essential oil which gives it its characteristic flavor probably makes it unpalatable to animals and at the same time preserves it from decay.

Date seeds are so hard and tough that they cannot be eaten and do not readily decay. Lemon, orange, horse-chestnut, and buckeye seeds are too bitter to be eaten, and the seeds of the apple, cherry, peach, and plum are somewhat bitter.

The seeds of larkspur (*Datura*),[1] croton, the castor-oil plant, nux vomica, and many other kinds of plants, contain active poisons.

[1] Commonly called Jimson weed.

CHAPTER III

MOVEMENTS, DEVELOPMENT, AND MORPHOLOGY OF THE SEEDLING

14. How the seedling breaks ground. As the student has already learned by his own observations, the seedling does not always push its way straight out of the ground. Corn, like all the other grains and grasses, sends a tightly rolled, pointed leaf vertically upward into the air; but seedlings in general are not found to do anything of the sort. The squash seedling is a good one in which to study what may be called the arched type of germination. If the seed when planted is laid horizontally on one of its broad surfaces, it usually goes through some such changes of position as are shown in Fig. 8.

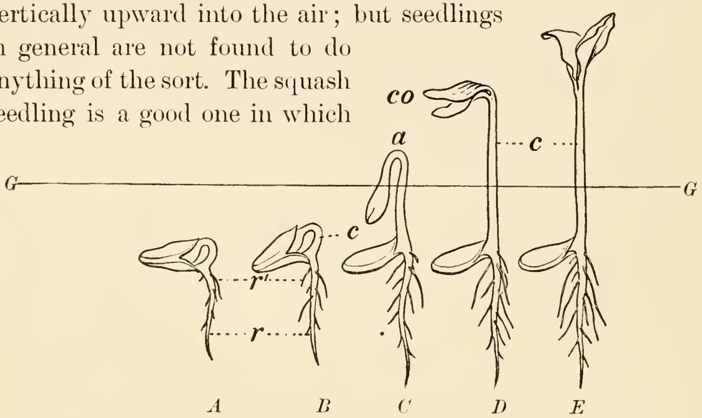

FIG. 8. Successive stages in the life history of the squash seedling

GG, the surface of the ground; *r*, primary root; *r′*, secondary root; *c*, hypocotyl; *a*, arch of hypocotyl; *co*, cotyledons

The seed is gradually tilted until, at the time of their emergence from the ground (at *C*), the cotyledons are almost vertical. The only part above the ground line *GG*, at this period, is the arched hypocotyl. Once out of ground, the cotyledons soon rise, until (at *E*) they are again vertical, but with the other end up from that which stood highest in *C*. Then the two cotyledons separate until they once more lie horizontally, pointing away from each other.

Whether the first part of the seedling to emerge from the ground is a pointed, rolled-up leaf, as in Indian corn, or the hypocotyl arch, as in Figs. 2 and 8, the result is to force the earth aside without injury to the plumule or the cotyledons.

15. What pushes the cotyledons up? A very little study of any set of squash seedlings, or even of Fig. 8, is sufficient to show that the portion of the plant where roots and hypocotyl are joined neither rises nor sinks, but that the plant grows both ways from this part (a little above r' in Fig. 8, *A* and *B*). It is evident that as soon as the hypocotyl begins to lengthen much it must do one of two things: either push the cotyledons out into the air or else force the root down into the ground as one might push a stake down. The plantlet, in passing from the stage shown at *A* to that of *B* and of *C*, develops many lateral roots, thus making it harder and harder for the root to be thrust bodily downward.

16. Getting rid of the seed coats. In seeds with thin coats the latter usually burst open irregularly and allow the opening cotyledons to escape. But in seeds with as thick a testa as that of the squash, and still more in the case of nuts, the cotyledons find their way out through a slit, or opening, which appears in a definite part of the seed. If for any reason the seed coat does not open, the embryo cannot grow. In many cases the moisture and freezing and thawing of a winter in the earth are almost essential to germination, and some seeds grow more promptly if they have been scorched by fire, or if they are cracked open before planting.

17. Discrimination between root and hypocotyl. It is not always easy to decide by their appearance and behavior what part of the seedling is root and what part is hypocotyl. In a seedling visibly beginning to germinate, the sprout, as it is commonly called, which projects from the seed might be either root or hypocotyl, or might consist of both together, so far as its appearance is concerned. A microscopic study of the cross section of a root, compared with one of the hypocotyl, would show decided differences of structure between the two. Their mode of growth is also different, as the pupil may infer from his own observations.

18. Final position of the cotyledons. As soon as the young plants of squash, bean, and pea have reached a height of three or four inches above the ground, it is easy to recognize important differences in the way in which they set out in life.

The cotyledons of the squash increase greatly in surface, acquire a green color and a generally leaf-like appearance, and, in fact, do the work of ordinary leaves. In such a case as this the appropriateness of the name *seed leaf* is evident enough, — one recognizes at sight the fact that the cotyledons are actually the plant's first leaves. In the bean the leaf-like nature of the cotyledons is not so clear. They rise out of the ground like the squash cotyledons, but then gradually shrivel away, though they may first turn green and somewhat leaf-like for a time.

In the pea, as in the acorn, the horse-chestnut, and many other seeds, we have quite another plan, — the underground type of germination. Here the thick cotyledons no longer rise above ground at all, because they are so gorged with food that they could never become leaves; but the young stem pushes rapidly up from the surface of the soil.

19. Development of the plumule. The development of the plumule seems to depend somewhat on that of the cotyledons. The squash seed has cotyledons which are not too thick to become useful leaves, and so the plant is in no special haste to get ready any other leaves. The plumule, therefore, cannot be found with the magnifying glass in the unsprouted seed, and is almost microscopic in size at the time when the hypocotyl begins to show outside of the seed coats.

In the bean, pea, and corn, on the other hand, since the cotyledons cannot serve as foliage leaves, the later leaves must be pushed forward rapidly. In the bean the first pair are already well formed in the seed. In the pea they cannot be clearly made out, since the young plant forms several scales on its stem before it produces any full-sized leaves, and the embryo contains only hypocotyl, cotyledons, and a sort of knobbed plumule, well developed in point of size, representing the lower, scaly part of the stem.

20. Root, stem, and leaf. By the time the seedling is well out of the ground the plant body, in most cases, possesses the three kinds of *vegetative organs*, or parts essential to growth, of ordinary seed plants; that is, the root, stem, and leaf, or, as they are sometimes classified, root and shoot. All of these organs may multiply and increase in size as the plant grows older, and their mature structure will be studied in later chapters; but some facts concerning them can best be learned by watching their growth from the outset.

21. Elongation of the root. We know that the roots of seedlings grow pretty rapidly from the fact that each day finds them reaching visibly farther down into the water or other medium in which they are planted. A sprouted Windsor bean in a vertical thistle tube will send its root downward fast enough so that ten minutes' watching through the microscope will suffice to show growth.

22. Root hairs. Very young seedlings of the grains, or of mustard or red clover, afford convenient material for studying *root hairs*. These are most abundantly developed when the seed is sprouted in air that is not very moist. Only a certain zone of the young root is covered with live hairs; the younger portions have not developed them and the older portions show only dead ones. Examination with a good lens or a low power of the microscope shows the gradual lengthening of the hairs, from very young ones near the root tip to full-grown ones farther up.

The root hairs in plants growing under ordinary conditions are surrounded by the moist soil and wrap themselves around microscopical particles of earth (Fig. 9). Thus they are able rapidly to absorb through their thin walls the soil water, with whatever mineral substances it has dissolved in it.

23. The young stem. The hypocotyl, or portion of the stem which lies below the cotyledons, is the earliest formed portion of the stem. Sometimes this grows but little; often, however, the hypocotyl lengthens enough to raise the cotyledons well above ground, as in Fig. 10.

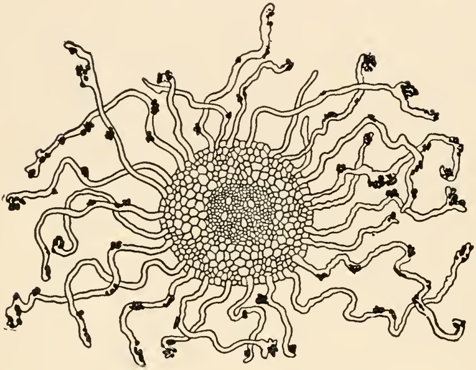

FIG. 9

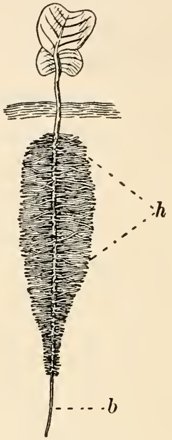

FIG. 10

FIG. 9. Cross section of a root

A good deal magnified, showing root hairs attached to particles of soil, and sometimes enwrapping these particles. — After Frank and Tschirch

FIG. 10. A turnip seedling, with the cotyledons developed into temporary leaves

h, root hairs from the primary root; *b*, bare portion of the root, on which no hairs have as yet been produced

The later portions of the stem are considered to be divided into successive sections called *nodes* (places at which a leaf, or a scale which represents a leaf, appears) and *internodes* (portions between the leaves).

The stem increases in length by the simultaneous elongation of several internodes, as shown by Fig. 11. It will be noticed that in the plant figured the greatest increase in length is neither in the oldest nor the youngest internodes which are growing at all, but in an intermediate region.

Every portion of the entire shoot, shown in the figure, has elongated except the interval 21–22.

Counting from the top the lengthening of several of the segments is as follows:

Intervals	Per Cent Increase in Length
1	100
2	120
3	140
4	140
5	160
6	140
7	120
8	110
9	110
10	100
11	80

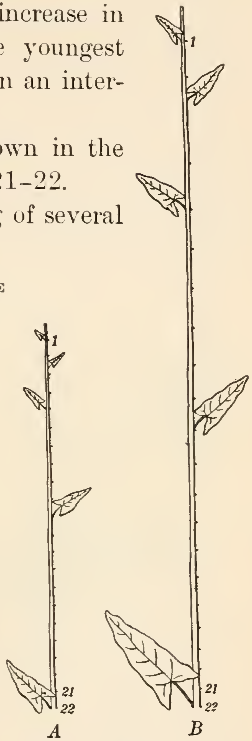

Fig. 11. Growth in a horizontal shoot of hedge bindweed[1]

A, the shoot divided by ink marks into 22 equal segments; *B*, the same, twenty-four hours later.—After Bonnier and Sablon

24. The first leaves. The cotyledons are, as already explained, the first leaves which the seedling possesses. Even if a plumule is found well developed in the seed, it was formed after the cotyledons. In those plants which have so much food stored in the cotyledons as to render them unfit ever to become useful foliage leaves, as in the pea, there is little or nothing in the color, shape, or general appearance of the cotyledon to make one think it really a leaf, and it is only by studying many cases that the botanist is enabled to class all

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[1] *Convolvulus sepium.*

cotyledons as leaves in their nature, even if they are quite unable to do the ordinary work of leaves. In seeds which have *endosperm*, or food stored outside of the embryo, the cotyledons usually become green and leaf-like, as they do, for example, in the four-o'clock, the morning-glory, and the buckwheat; but in the seeds of the true grains, which contain endosperm, as in the familiar instance of Indian corn, a large portion of the single cotyledon remains throughout as a thickish mass buried in the seed. In a few cases, as in the pea, there are scales instead of true leaves formed on the first nodes above the cotyledons, and it is only at about the third node above that leaves of the ordinary kind appear. In the bean and some other plants which in general bear one leaf at a node along the stem, there is a pair produced at the first node above the cotyledons, and the leaves of this pair differ in shape from those which arise from the succeeding portions of the stem.

Fig. 12. Germinating pine
co, cotyledons

25. Classification of plants by the number of their cotyledons. In the pine family the germinating seed often displays more than two cotyledons, as shown in Fig. 12; in the majority of common seed plants the seed contains two cotyledons, while in the lilies, the rushes, the sedges, the grasses, and some other plants there is but one cotyledon. Upon these facts is based the division of most seed plants into two great groups: the *dicotyledonous plants*, which have two seed leaves, and the *monocotyledonous plants*, which have one seed leaf. Other important differences nearly always accompany the difference in number of cotyledons, as will be seen later.

CHAPTER IV

ROOTS

26. Origin of roots. The *primary root* originates from the lower end of the hypocotyl, as the student learned from his own observations on sprouting seeds. The branches of the primary root are called *secondary roots,* and the branches of these are known as *tertiary roots.* Those roots which occur on the stem or in other unusual places are known as *adventitious roots.* The roots which form so readily on cuttings of willow, southernwood, Tropæolum, French marigold, cultivated "geranium" (Pelargonium), Tradescantia, and many other plants, when placed in damp earth or water, are adventitious.

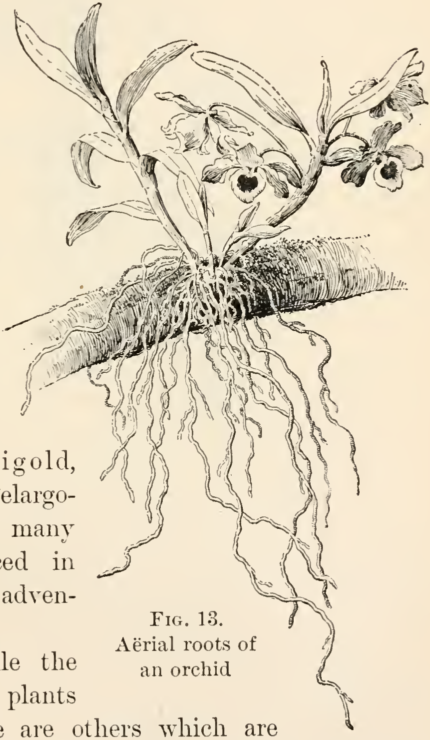

Fig. 13.
Aërial roots of an orchid

27. Aërial roots. While the roots of most familiar plants grow in the earth, there are others which are formed in the air, called *aërial roots.* They serve various purposes: in some tropical air plants (Fig. 13) they fasten the plant to the tree on which it establishes itself, as well as take in water which drips from branches and trunks above them, so that these plants require no soil and grow suspended in mid air from trees which serve them merely as supports; many such air plants are grown in greenhouses. In such plants as the ivy (Fig. 14) the aërial roots, which are also adventitious, hold the plant to the wall or other surface up which it climbs.

In the Indian corn (Fig. 15) roots are sent out from nodes at some distance above the ground and descend until they enter the ground. They serve to anchor the cornstalk so that it may resist the wind, and to supply additional water to the plant. They often produce no rootlets until they reach the ground.

Fig. 14. Aërial, adventitious roots of the ivy

28. Water roots. Many plants, such as the willow, readily adapt their roots to live either in earth or in water, and some, like the little floating duckweed, regularly produce roots which are adapted to live in water only. These water roots often show large and distinct sheaths on the ends of the roots, as, for instance, in the so-called water hyacinth (*Eichhornia*).

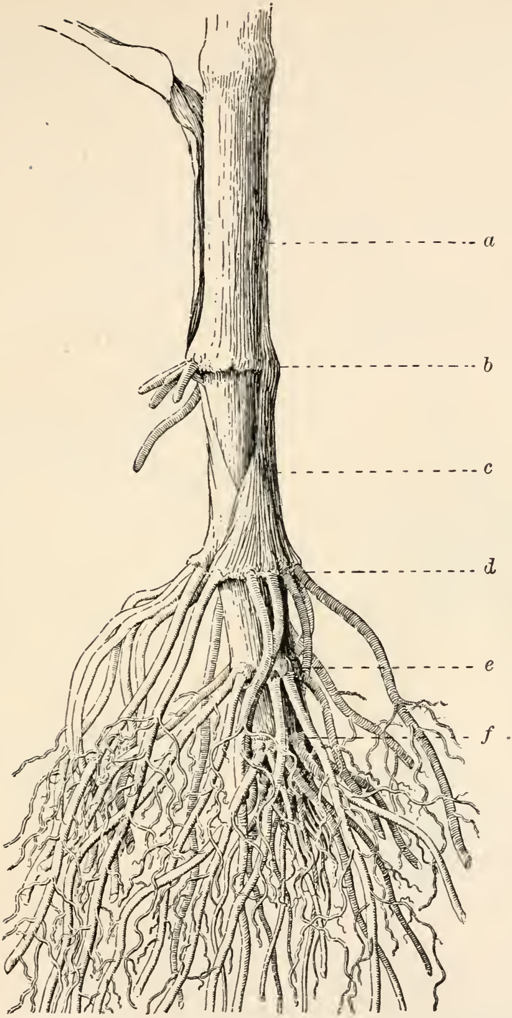

Fig. 15. Lower part of stem and roots of Indian corn, showing aërial roots ("brace roots")

a, *c*, internodes of the stem; *b*, *d*, *e*, *f*, nodes of various age bearing roots. Most of these started as aërial roots, but all except those from *b* have now reached the earth

29. Parasitic roots. The dodder, the mistletoe, and a good many other seed plants are called *parasites*, since they live, at least in part, upon food which they steal from other plants called their *hosts*. Parasites develop peculiar roots, which penetrate the tissues of the host and form most intimate connections with the interior portions of the stem or root of the latter.

Fig. 16. Dodder, a parasitic seed plant

A, magnified section of stem penetrated by roots of dodder; *B*, dodder upon a golden-rod stem; *C*, seedling dodder plants growing in earth; *h*, stem of host; *l*, scale-like leaves; *r*, sucking roots, or *haustoria;* *s*, seedlings. — *A* and *C* after Strasburger

In the dodder, as is shown in Fig. 16, the seedling parasite is admirably adapted to the conditions under which it is to live. Rooted at first in the ground, it develops a slender, leafless stem, which, leaning this way and that, no sooner comes into permanent contact with a congenial host than it produces sucking roots at many points, gives up further growth in its soil roots, and lengthens rapidly on the strength of the supplies of ready-made sap which it obtains from the host.

30. Forms of roots. The primary root is that which proceeds like a downward prolongation directly from the lower end of the hypocotyl. In many cases the mature root system of the plant contains one main root much larger than any of its branches. This is called a *tap root* (Fig. 17).

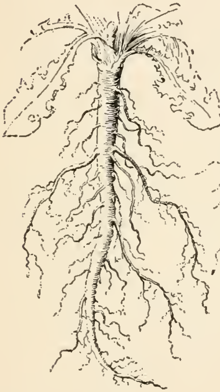

Fig. 17
A tap root

Fig. 18
Fibrous roots

Fig. 19
Fleshy and clustered roots

Such a root, if much thickened, may assume some such form as that of the carrot, parsnip, beet, turnip, or radish, and is called a *fleshy* root. Some plants produce a cluster of roots from the lower end of the hypocotyl. Such roots often become thickened, as in the sweet potato and the dahlia (Fig. 19).

Roots of grasses, etc., are thread-like, and known as *fibrous roots* (Fig. 18).

31. General structure of roots. The general structure of the very young root can be partially made out by examining the entire root with a moderate magnifying power. Often the whole is sufficiently translucent to allow the interior as well as the exterior portion to be studied while the root is still alive and growing.

The main bulk of the root is composed of a central cylinder and the cortical portion which surrounds it. The outermost part of the *cortex* is a layer of cells forming a thin skin known as the *epidermis.* The tip of the root is covered by a mass of loosely attached cells forming the protective *root cap.*

On examining Figs. 20 and 21, the cylinders of which the root is made up are easily distinguished, and the main constituent parts of each can be made out without much trouble. The epidermal cells are seen to be somewhat brick-shaped, many of them provided with extensions into root hairs. Inside the epidermis lie several layers of rather globular, thin-walled cells, and inside these a boundary layer between the cortical or bark portion of the root and the central cylinder. This latter region is especially marked by the presence

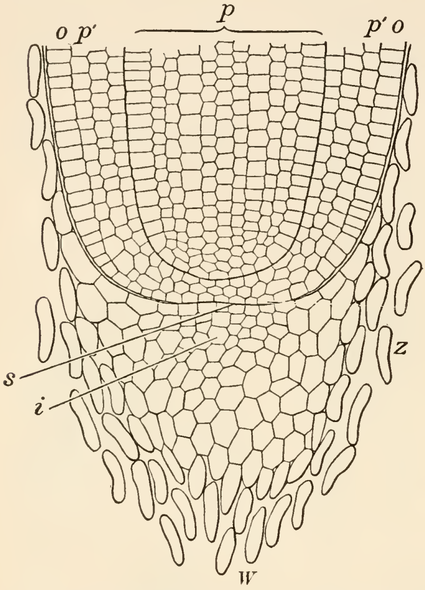

Fig. 20. Lengthwise section (somewhat diagrammatic) through root tip of Indian corn. × about 130

W, root cap; *i*, younger part of cap; *z*, dead cells separating from cap; *s*, growing point; *o*, epidermis; *p′*, intermediate layer between epidermis and central cylinder; *p*, central cylinder, in which the fibro-vascular bundles arise. — After Wiesner of certain groups of cells, shown at *w*, *d*, and *b* (Fig. 21), the two former serving as channels for air and water, the latter (and *w* also) giving toughness to the root.

Roots of shrubs and trees more than a year old will be found to have increased in thickness by the process described in Chapter VII, and a section may look unlike that shown in Fig. 21.

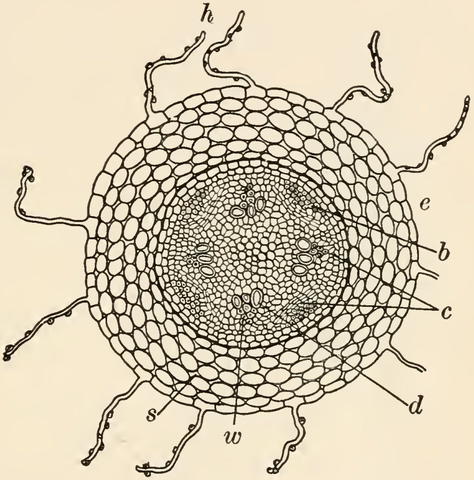

FIG. 21. Much magnified cross section of a young dicotyledonous root

h, root hairs with adhering bits of sand; *e*, epidermis; *s*, thin-walled, nearly globular cells of bark; *b*, hard bast; *c*, cambium; *w*, wood cells; *d*, ducts

32. Storage of reserve material in roots. Many roots contain large quantities of stored plant food, usually in the shape of starch, sugar, proteids, or all three together. Parsnips, carrots, turnips, and sweet potatoes are familiar examples of storage roots.

Beet roots contain so much sugar that a large part of the sugar supply of Europe, and an increasing portion of our own supply, is obtained from them. Oftentimes the bulk of a fleshy root is exceedingly large as compared with that of the parts of the plant above ground.

Not infrequently roots have a bitter or nauseous taste, as in the case of the chicory, the dandelion, and the rhubarb; and a good many, like the monkshood, the yellow jasmine, and the pinkroot, are poisonous. Evidently the plant may be benefited by the disgusting taste or poisonous nature of its roots, which renders them uneatable.

33. Use of the food stored in fleshy roots. The parsnip, beet, carrot, and turnip are *biennial plants;* that is, they do not produce seed until the second summer or fall after they are planted.

The first season's work consists mainly in producing the food which is stored in the roots. To such storage is due their characteristic fleshy appearance. If the root is planted in the following spring, it feeds the rapidly growing stem which proceeds from the bud at its summit, and an abundant crop of flowers and seed soon follows; while the root, if examined in late summer, will be found to be withered, with its store of reserve material quite exhausted.

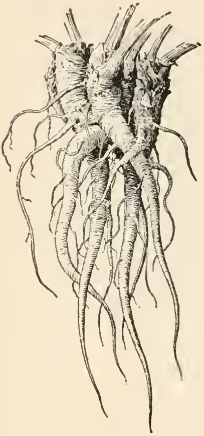

Fig. 22. Fleshy roots of garden rhubarb. About one fifteenth natural size

The roots of the rhubarb (Fig. 22), the sweet potato, and of a multitude of other *perennials,* or plants which live for many years, contain much stored plant food. Many such plants die to the ground at the beginning of winter, and in spring make a rapid growth from the materials laid up in the roots.

34. Extent of the root system. The total length of the roots of ordinary plants is much greater than is usually supposed. They are so closely packed in the earth that only a few of the roots are seen at a time during the process of transplanting, and when a plant is pulled or dug up in the ordinary way a large part of the whole mass of roots is broken off and left behind. A few plants have been carefully studied to ascertain the total weight and length of the roots. Those of winter wheat have been found to extend to a depth of seven feet. By weighing the whole root system of a plant, and then weighing a known length of a root of average diameter, the total length of the roots may be estimated. In this way the roots of an oat plant have been calculated to measure about

154 feet; that is, all the roots, if cut off and strung together end to end, would reach that distance.

Single roots of large trees often extend horizontally to great distances, but it is not often possible readily to trace the entire depth to which they extend. One of the most notable examples of an enormously developed root system is found in the mesquite of the far Southwest and Mexico. When this plant grows as a shrub, reaching the height, even in old age, of only two or three feet, it is because the water supply in the soil is very scanty. In such cases the roots extend down to a depth of sixty feet or more, until they reach water, and the Mexican farmers in digging wells follow these roots as guides. Where water is more abundant, the mesquite forms a good-sized tree, with much shorter roots.

35. The absorbing surface of roots. The soil roots of most seed plants are provided with a highly efficient means for absorbing water in the shape of a coating of *root hairs*, with which their younger portions are thickly covered. Some idea of their abundance may be gathered from the estimate that on the hair-bearing portions of the roots of the common pea about 1437 hairs occur on every hundredth of a square inch of surface.

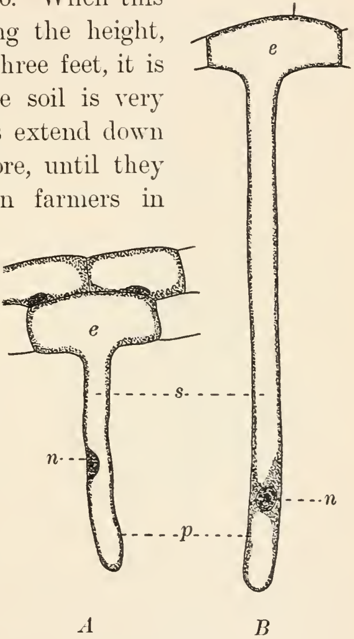

FIG. 23

A, a very young root hair; *B*, an older one (both greatly magnified); *e*, cells of the epidermis of the root: *n*, nucleus; *s*, watery cell sap; *p*, protoplasm lining the cell wall. — After Frank

A root hair is an extremely thin-walled tube, springing from an epidermal cell, into which it opens. The way in which the cells give rise to hairs is well shown in Figs. 21 and 23.

Most water roots are destitute of root hairs, and absorb water through the general epidermal surface of their younger portions.

Aërial roots, like those shown in Fig. 13, are in many cases provided with an external absorbent layer of spongy tissue, by means of which they retain some of the water which trickles down them during rains. This stored moisture they gradually give up to the plant.

36. Absorption of water by roots. Just how much water some kinds of plants give off (and therefore absorb) per day will be discussed when the uses of the leaf are studied. For the present it is sufficient to state that even an annual plant during its lifetime absorbs through the roots very many times its own weight of water. Grasses have been known to take in their weight of water in every twenty-four hours of warm, dry weather. This absorption in most soil roots takes place mainly through the root hairs. Their walls are extremely thin, and have no holes or pores visible under even the highest power of the microscope, yet the water of the soil penetrates very rapidly to the interior of the root hairs. The soil water brings with it all the substances which it can dissolve from the earth about the plant; and the closeness with which the root hairs cling to the particles of soil, as shown in Figs. 9 and 21, must cause the water which is absorbed to contain more foreign matter than underground water in general does, particularly since the roots give off enough weak acid from their surface to corrode the surface of stones which they enfold or cover.

37. Substances required by the plant for nutrition. Ordinary seed plants require for their nutrition ten of the chemical elements. By far the greater part of the weight of the plant body is usually due to compounds of *carbon*, *hydrogen*, *oxygen*, and *nitrogen*. Besides these there are present the six elements, — *sulphur*, *phosphorus*, *potassium*, *calcium*, *magnesium*, and *iron*. In ordinary green meadow grass there is about 80 per cent of water and 20 per cent of dry matter. On drying the grass into hay and then burning the latter, some 2 per cent of ash will remain, and in this will be found the six elements — sulphur, phosphorus, potassium, calcium, magnesium, and iron — in the form of incombustible salts (sulphates, phosphates, and so on).

The plant gets its carbon and oxygen from the air, as will be explained in Chapter XII. Deprived of air, all green plants soon die. The hydrogen is obtained from water.

The importance of the six ash-forming constituents mentioned above is most readily studied by means of water cultures in which plants are grown with suitable proportions of dissolved salts. If any one of the six elements is omitted from a solution, the plants grown in it are dwarfish and unhealthy.

Ordinary soil water contains sufficient salts in solution for the nutrition of plants, but not always enough to stimulate rapid growth.

38. Sap pressure. Not only does much water gain admission to the plant through the roots, but under ordinary circumstances it is found forcing its way on, into, and through the stem (for explanation see Secs. 48–51). The force called *sap pressure* with which the upward-flowing current of water presses may be estimated by attaching a mercury gauge to the root of a tree or the stem of a small sapling. This is best done in early spring after the thawing of the ground, but before the leaves have appeared. The experiment may also be performed indoors upon almost any plant with a moderately firm stem, through which the water from the soil rises freely.

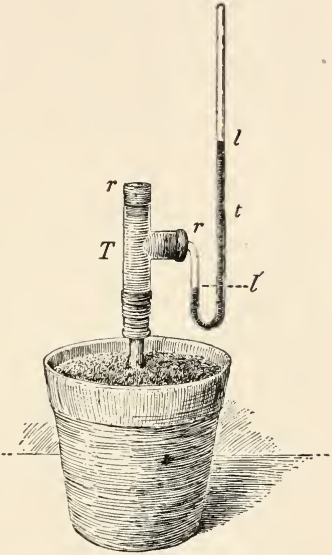

Fig. 24. Apparatus to measure sap pressure

T, large tube fastened to the stump of the dahlia stem by a rubber tube; *r*, *r*, rubber stoppers; *t*, bent tube containing mercury; *l′*, *l*, upper and lower level of mercury in *T*. — After Sachs

A dahlia plant or a tomato plant answers well, though the sap pressure from one of these will not be nearly as great as that from a larger shrub or a tree growing out of doors. In Fig. 24 the apparatus is shown attached to the stem of a dahlia. The difference of level of the mercury in the bent tube serves to measure the pressure. For every foot of difference in level there must be a pressure of nearly six pounds per square inch on the stump at the base of the tube *T*.[1]

A black birch root tested at the end of April has given a sap pressure of thirty-seven pounds to the square inch. This would sustain a column of water about eighty-six feet high.

39. Root absorption and temperature of the soil. The temperature of roots and the earth about them has much to do with the rate at which they absorb water. Some plants can absorb it at temperatures as low as 25° F. (– 4° C.), while others cannot do so at any temperature below 39° F. (4° C.). This fact of the power to get water from the soil ceasing at temperatures in the neighborhood of the freezing point has most important consequences, since it implies that a plant may die for lack of water with its roots immersed in cold, wet soil. Hence the parched appearance often noticed in leaves killed by frost.

40. Movements of young roots. The fact that roots usually grow downward is so familiar that we do not generally think of it as a thing that needs discussion or explanation. Since they are pretty flexible, it may seem as though young and slender roots merely hung down by their own weight, like so many bits of wet cotton twine. But the root of a young Windsor bean seedling or of a sprouting pea will force itself down into mercury. By comparing the weights of equal bulks of mercury and Windsor bean roots, it is found that the mercury is about fourteen times as heavy as the substance of the roots. Evidently, then, the submerged part of the root must have been held under by a force about fourteen times its own weight.

[1] For a more accurate method see *Handbook*.

A more accurate measurement of the force exerted by the root may be made by confining it so it cannot bend, and letting it push down on a spring. In this way it is found that the root of the Windsor bean can push with a pressure of about ten ounces.

Making fine equidistant cross marks with ink along the upper and the lower surface of a root that is about to bend downward at the tip readily shows that those of the upper series soon come to be farther apart, — in other words, *that the root is forced to bend downward by the more rapid growth of its upper as compared with its under surface.*

41. Geotropism. The property which plants or their organs manifest, of assuming a definite direction with reference to gravity,[1] is called *geotropism.* When, as in the case of the primary root, the effect of gravity is to make the part, if unobstructed, turn or move downward, we say that the geotropism is *positive.* If the tendency is to produce upward movement, we say that the geotropism is *negative;* if horizontal movement, that it is *lateral.* It was stated in the preceding section that the direct cause of the downward extension of roots is unequal growth. We might easily suppose that this unequal growth is not due to gravity, but to some other cause. To test this supposition, the simplest plan, if it could be carried out, would be to remove the plants studied to some distant region where gravity does not exist. This of course cannot be done, but we can easily turn a young seedling over and over so that gravity will act on it now in one direction, now in another, and so leave no more impression than if it did not act at all. Or we can whirl a plant so fast that not only is gravity done away with, but another force is introduced in its place. If a vertical wheel, like a carriage wheel, were provided with a few loosely fitting iron rings strung on the spokes, when the wheel was revolved rapidly the rings would all fly out to the rim of the wheel. So in Fig. 25 it will

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[1] Gravity means the pull which the earth exerts upon all objects on or near its surface.

be noticed that the growing tips of the roots of the sprouting peas point almost directly outward from the center of the disk on which the seedlings are fastened. In this case the so-called "centrifugal force" due to the rotation of the wheel is sufficient wholly to overcome geotropism.

Fig. 25. Sprouting peas on a rapidly whirling disk

The youngest portions of the roots all point directly away from the axis about which they were revolved. — After Detmer

42. Direction taken by secondary roots. As the student has already noticed in the seedlings which he has studied, the branches of the primary root usually make a considerable angle with it (Fig. 2). Often they run out for long distances almost horizontally. This is especially common in the roots of forest trees, above all in cone-bearing trees, such as pines and hemlocks (Fig. 26). This horizontal, or nearly horizontal, position of large secondary roots is the most advantageous arrangement to make them useful in staying or guying the stem above to prevent it from being blown over by the wind.

Fig. 26. Roots of a white pine

43. Fitness of the root for its position and work. The distribution of material in the woody roots of trees and shrubs and their behavior in the soil show many adaptations to the conditions by which the roots are surrounded. The growing tip of the root, as it pushes its way through the soil, is exposed to bruises; but these are largely warded off by the root cap. The tip also shows a remarkable sensitiveness to contact with hard objects, so that when touched by one it swerves aside and thus finds its way downward by the easiest path. Roots with an unequal water supply on either side grow toward the moister soil; when unequally heated they grow in the direction of the most desirable temperature, and they usually grow away from the light. Roots are very tough, because they need to resist strong pulls, but not as stiff as stems and branches of the same size, because they do not need to withstand sidewise pressure, acting from one side only. The corky layer which covers the outsides of roots is remarkable for its power of preventing evaporation. It must be of use in retaining in the root the moisture which otherwise must be lost on its way from the deeper rootlets (which are buried in damp soil), through the upper portions of the root system, about which the soil is often very dry.

CHAPTER V

SOME PROPERTIES OF CELLS AND THEIR FUNCTIONS IN THE ROOT

44. Definition of cell. This is not the best place to consider the nature of cells in much detail (see Chapter XVIII); but some of the facts learned in Chapter IV cannot be understood without a few words of explanation of cell structure and functions.

Protoplasm is the nitrogenous living substance of which the most rapidly growing parts of plants are mainly composed. The activities of the plant are due to the peculiar qualities and powers of protoplasm. *A cell is a unit of protoplasm, called a protoplast.* The protoplast of plants is usually inclosed in a case or covering whose walls (*cell walls*) are composed of a substance known as *cellulose.* Each protoplast usually contains a single denser protoplasmic structure, called the *nucleus.*

In form and size cells vary greatly. Those of the root hair (Fig. 23) are good examples of the slender, thread-like form; those of Fig. 27 well illustrate forms commonly assumed when cells are pressed upon by others on all sides, as they usually are in the interior portions of the organs of higher plants.

45. Growth and reproduction. The most remarkable property of cells is their power of growth and reproduction. Growth results not only from an increase in the size of cells but also in their number as a result of *cell division.* This is the separation of a protoplast, generally into two independent protoplasts or daughter cells, and is the fundamental cause of all growth and development. The full-grown seed plant, composed of millions of cells, arises from the embryo (with perhaps only a few thousand), which had its beginning in a single cell. Cell division is preceded by division of the nucleus (Fig. 170).

Reproduction, or the formation of new organisms similar to the parents, is possible only for protoplasm, not for any other known substance.

46. Irritability. Another characteristic of protoplasm is its *irritability.* By this is meant its power of responding in some way to an application of energy which serves as a *stimulus.* A famous plant physiologist[1] has illustrated the matter very simply thus: A wound-up alarm clock, which is not going, is given a shake (stimulus), which starts the clock, and after an interval of time (latent period) rings the alarm (result). The sensitiveness of the clock to any jar which sets it going corresponds to the irritability of living protoplasm. This extremely delicate responsiveness may be manifested in a simple cell or in an organ or entire plant composed of multitudes of cells.

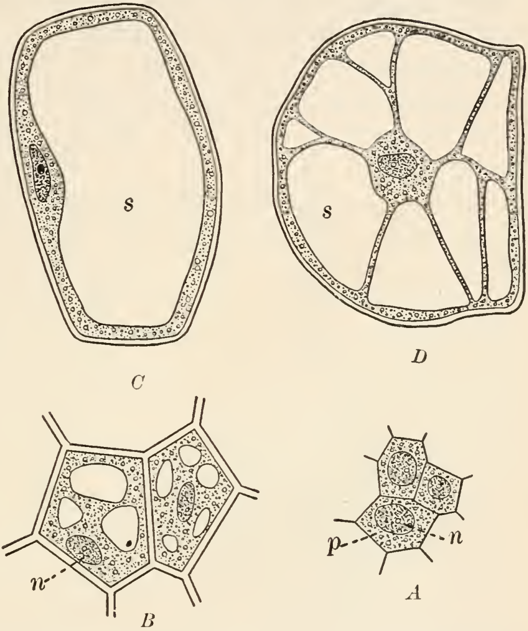

Fig. 27. Protoplasts in ovule and fruit of snowberry (*Symphoricarpus racemosus*)

A, cells from ovule (× 340); *B*, cells from an ovule further developed (× 340); *C*, *D*, cells from pulp of fruit (× 110); *n*, nucleus; *p*, protoplasm; *s*, cell sap. — After Prantl

In the young and rapidly growing cells *A* and *B* the cell sap is not present, or present only in small quantities, while in the older cells *C* and *D* it occupies a large portion of the interior of the cell

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[1] Professor W. Pfeffer, of Leipzig, Germany.

Some of the most important stimuli which call out manifestations of irritability in protoplasm are heat, light, electricity, gravity, pressure of external objects, and contact with substances which act chemically on the protoplasm. Many instances of irritability will come up in later chapters. A notable example of response to a stimulus is the beginning of germination in seeds subjected to a suitable degree of heat in presence of moisture.

The ways in which the responses to stimulation may show themselves are very numerous, and the same individual or organ may be favorably affected by a certain amount of a given stimulus and unfavorably by a greater amount of the same stimulus. Every one has had the experience of drawing near to a moderately heated stove in cold weather and then retreating from it when the fire grew too hot. So, too, certain microscopic unicellular plants, living in water, move toward the light until it reaches a certain intensity, but when that intensity is passed, they move in the opposite direction, toward the dark.

47. Selective absorption. Another extremely important power of live protoplasm is that of *selective absorption.* By this is meant the ability to take up from liquids or gases certain substances and leave unabsorbed other elements or compounds which are also present.

Thus plants of two different species, both growing in the same soil, usually take from it very various amounts or kinds of mineral matter. For instance, barley plants in flower and red clover plants in flower contain about the same proportion of mineral matter (left as ashes after burning). But the clover contains $5\frac{2}{3}$ times as much lime as the barley, and the latter contains about 18 times as much silica as the clover. This difference must be due to the selective action of the protoplasm in the absorbing cells of the roots.

48. Osmosis. The process by which two liquids of different densities separated by membranes pass through the latter and mingle, as soil water does with the liquid contents of root hairs, is called *osmosis.* It is readily demonstrated by experiments with thin animal or vegetable membranes. For instance, when prunes, raisins, or other dried fruit, are put in water to soak, water penetrates the outer skin and swells the seed or fruit, while some of the material from within comes out through the skin and flavors or discolors the water. If whole cranberries, cherries, or plums are put into boiling sirup, a similar exchange takes place, but in this case the fruit is shriveled.

A still better experiment is that with an egg from which a bit of the shell has been chipped away at the bottom, arranged as shown in Fig. 28. The entrance of water is shown by the rise of some of the contents of the egg in the tube.

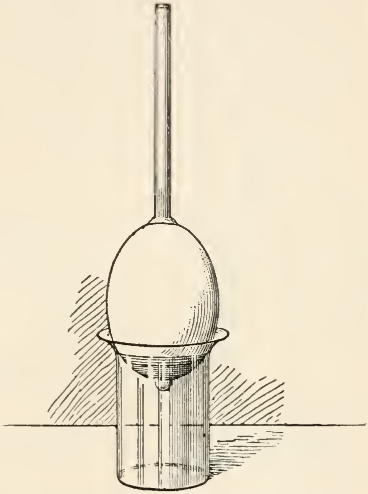

FIG. 28. Egg on beaker of water, to show osmosis

The tube is cemented to the eggshell, into which it opens. At the bottom a large piece of the shell has been chipped away, leaving the thin skin which lines the egg in contact with the water in the beaker

49. Inequality of osmotic exchange. The nature of the two liquids separated by any given membrane determines in which direction the greater flow shall take place unless what would naturally be the direction of flow is overruled by the selective action of living protoplasm.

If one of the liquids is pure water and the other is water containing solid substances dissolved in it, the greater flow of liquid will be away from the pure water into the solution, and the stronger or denser the latter, the more unequal will be the flow. This principle is well illustrated by the egg-osmosis experiment. Another important principle is that substances which readily crystallize and are easily soluble, like salt or sugar, pass rapidly through membranes, while jelly-like substances, like white of egg, can hardly pass through them at all.

50. Study of osmotic action of living protoplasm; plasmolysis. The obvious parts of most living and growing plant cells are a cell wall, which is a skin or inclosure made of *cellulose*, and the living, active cell contents, or *protoplasm* (Sec. 44). Every one is familiar with cellulose in various forms, one of the best examples being that afforded by clean cotton. It is a tough, white, or colorless substance, and chemically rather inactive. Often, in living cells, the spaces between strands and protoplasmic lining are filled with a watery liquid called the *cell sap*.

The action of living protoplasm in controlling osmosis is well shown by the process known as *plasmolysis*.

If thin-walled cells with liquid or semi-liquid protoplasm, such as those of one of the pond scums, are put into a salt solution, the cell contents will shrink away from the cell wall (Fig. 168, *B*) because the direction of flow, toward the denser liquid, draws water out of the cell. Repeating the experiment with a cell which has been killed by a few minutes' immersion in a poisonous solution (e.g. of chromic acid) shows no plasmolysis.

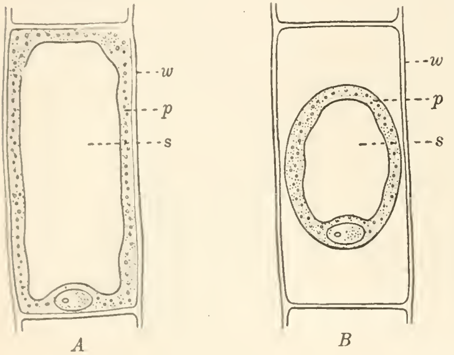

FIG. 29. Cells from root of Indian corn

A, in natural condition; *B*, plasmolyzed in 5 per cent solution of potassium nitrate; *w*, cell wall; *p*, denser part of protoplasm; *s*, cell sap. Much magnified. — After Pfeffer

So, too, slices of a red beet impart little color to water in which they are placed, but after the cells are killed by boiling the color comes out freely.

51. Osmosis in root hairs. The soil water, practically identical with ordinary spring or well water, is separated from the more or less sugary or mucilaginous sap inside of the root hairs only by their delicate cell walls, lined with a thin layer of protoplasm. This soil water will pass rapidly into the plant, while very little of the sap will come out. The selective action, which causes the flow of liquid through the root hairs to be almost wholly inward, is due to the living layer of protoplasm, which covers the inner surface of the cell wall of the root hair. Traveling by osmotic action from cell to cell, a current of water derived from the root hairs is forced up through the roots and into the stem, somewhat as the contents of the egg was forced up into the tube shown in Fig. 28.

But there is this important difference in the two cases, that while the process in the tube was all due to the impulse received at the start from the egg membrane, in the plant stem the original pressure due to osmosis in the root hairs may be affected by osmosis in countless thousands of cells higher up.

52. Behavior of roots due to irritability. In Chapter IV a little was said about the geotropism of roots, their tendency to put themselves into the most favorable conditions as regards moisture, heat, and light, and their manner of avoiding obstacles. All these actions are manifestations of irritability.

The subject of geotropism of roots is a very complicated one, but it seems pretty certain that *gravity somehow acts as a stimulus on the sensitive cells of the root tip, this stimulus is transmitted to the cells of the most rapidly growing portion of the root (a little farther back), unequal growth of the upper and under cells of this portion follows, and so the root is bent, if its position is not vertical in the beginning.*

Moisture and heat (in the case of Indian corn up to 99.5° F. or 37.5° C.) are favorable to the growth of roots, and so as stimuli produce growth toward the source of moisture or heat, while light is usually slightly unfavorable and therefore generally results in growth of the root toward darkness.

CHAPTER VI

STEMS

53. Nature of the stem. The work of taking in the raw materials which the plant makes into its own food is done mainly by the roots and the leaves. These raw materials are taken from earth, from water, and from the air (see Chapter XII). The stem is that part or organ of the plant which serves to bring roots and leaves into communication with each other. In most seed plants the stem also serves the important purpose of lifting the leaves up into the sunlight, where they can best do their special work.

The student has already, in Chapter III, learned something of the development of the stem and the seedling; he has now to study the external and internal structure of the mature stem. Much in regard to this structure can be learned most easily from the examination of twigs and branches of our common forest trees in their winter condition.

FIG. 30. A quickly grown twig of cherry, with lateral and terminal buds in October

b sc, bud-scale scars. All above these scars is the growth of the spring and summer of the same year

54. Position of leaf buds. The winter buds of most of our trees and shrubs are formed at points on the twig just above the origins of the leafstalks, as shown in Fig. 79. After the fall of the leaves the buds by their positions indicate where the leaves were formerly attached. They may be arranged in pairs, a bud on one side of the stem and its mate exactly opposite, or they may form a spiral around the stem, as shown in Fig. 30. Since every leaf bud — that is, every bud which contains rudimentary leaves — will, if successful, grow into a branch, the position of the buds is most important in determining the shape of the tree.

55. Opposite branching. Trees with opposite leaves and buds show a tendency to form twigs in four rows about at right angles to each other along the sides of the branch, as shown in Fig. 31.

This arrangement will not usually be perfectly carried out, as most of the buds never grow, since they are shaded and starved, or some may grow much faster than others and so make the plan of branching less evident than it would be if all grew alike.

Fig. 31. Opposite branching in a very young sapling of ash

Fig. 32. Alternate branching in a very young apple tree

56. Alternate branching. In trees like the beech the twigs will be found to be arranged in a more or less regular spiral line about the branch. This, which is known as the *alternate* arrangement (Fig. 32), is more commonly met with in trees and shrubs than the *opposite* arrangement. It admits of many varieties, since the spiral may wind more or less rapidly round the stem. In the apple, pear, cherry, poplar, oak, and walnut, one passes over five spaces before coming to a leaf which is over the first, and in doing this it is necessary to make two complete turns around the stem (Fig. 100).

57. Growth of the terminal bud. In some trees the terminal bud from the outset keeps the lead and produces a slender, upright tree (Fig. 33), as in the pines, spruces, and firs.

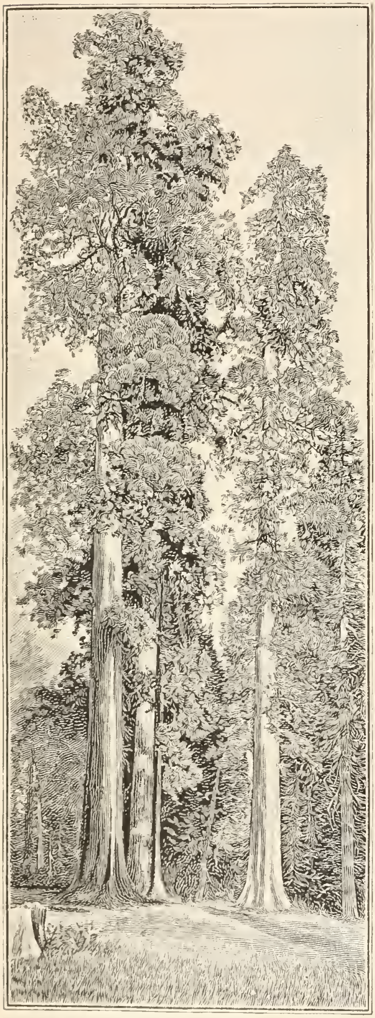

Fig. 33. California giant redwoods (*Sequoia*), illustrating upright growth

After J. H. White

In such trees as the apple and many oaks the terminal bud has no preëminence over others, and the form of the tree is round-topped and spreading (Fig. 34). Most forest trees are intermediate between these extremes.

Branches owe their characteristics to several factors. Most of our trees and larger shrubs make a *definite annual growth,* with the buds ripened before the coming of winter (Fig. 79). In these the terminal bud is likely to grow and continue the branch. Such shrubs and trees as the raspberry and blackberry, the sumach and the ailanthus, make an *indefinite annual growth,* that is, the tips of the branches are usually killed by frost, and so the tree forks often. Terminal flower buds (Figs. 36, 37) also cause forking and allow the tree to form no long, straight branches.

If the terminal buds of branches keep the lead of the

Fig. 34. An American elm, illustrating spreading growth

lateral ones, but the latter are numerous and most of those which survive grow into slender twigs, the delicate spray of the elm and many birches is produced (Fig. 38).

The general effect of the branching depends much upon the angle which each branch or twig forms with that one from which it springs. The angle may be quite acute, as in the birch (Fig. 38); or more nearly a right angle, as in the ash (Fig. 31). The inclination of lateral branches is due to geotropism, just as is that of the branches of primary roots. The vertically upward direction of the shoot which grows from the terminal bud is also due to geotropism, which, however, in the shoot, is exactly opposite to that in the root.

This is really only a brief way of saying that the growing tip of the main stem of the tree, or of any branch, is made to take and keep its proper direction, whether vertically upward or at whatever angle is desirable for the tree, by the steering action of gravity. After growth has ceased this steering action can no longer be exerted, and so a tree that has been bent over — as, for instance, by a heavy load of snow — cannot right itself unless it is elastic enough to spring back when the load is removed. The tip of the trunk and of each branch can grow and thus become vertical, but the old wood cannot do so.

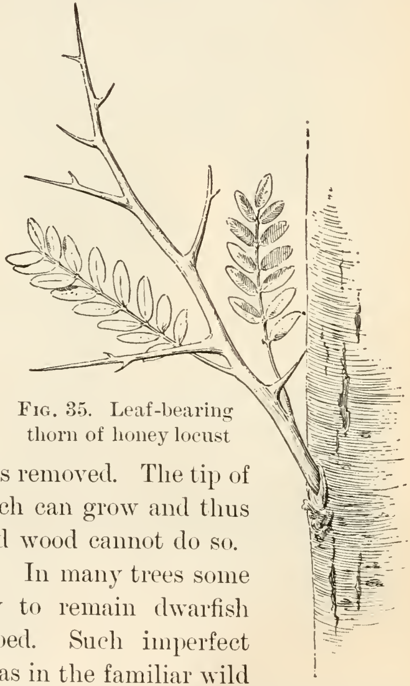

Fig. 35. Leaf-bearing thorn of honey locust

58. Thorns as branches. In many trees some branches show a tendency to remain dwarfish and incompletely developed. Such imperfect branches may form thorns, as in the familiar wild crab-apple trees and in the pear trees which occur in old pastures in the northeastern states. In the honey locust very formidable branching thorns spring from adventitious or dormant buds on the trunk or limbs. They sometimes show their true nature as branches by bearing leaves (Fig. 35).

59. Trees, shrubs, and herbs. Plants of the largest size, with a main trunk of a woody structure, are called *trees*. *Shrubs* differ from trees in their smaller size, and generally in having several stems which proceed from the ground or near it, or in having much-forked stems. The witch-hazel, the dogwoods, and the alders, for instance, are most of them classed as shrubs for this reason, though in height some of them equal the smaller trees. Some of the smallest shrubby plants, like the dwarf blueberry, the wintergreen, and the trailing arbutus, are only a few

Fig. 36. Tip of a branch of magnolia, illustrating forking due to terminal flower buds

A, oldest flower-bud scar; *B*, *C*, *D*, scars of successive seasons after *A*; *L*, leaf buds; *F*, flower buds inches in height, but are ranked as shrubs because their woody stems do not die to the ground in winter.

Herbs are plants whose stems above ground die every winter.

60. Annual, biennial, and perennial plants. *Annual* plants are those which live but one year, *biennials* those which live two years or nearly so.

Some winter annuals do not flower until their second summer. This is true of the evening primrose and the fringed gentian, and of winter wheat and rye among cultivated plants.

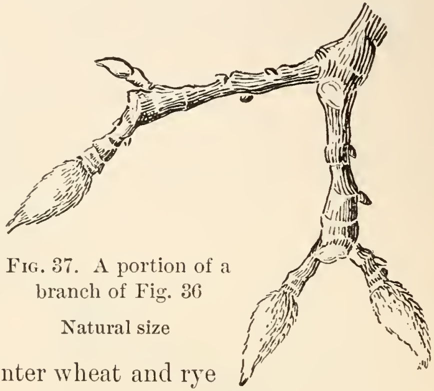

Fig. 37. A portion of a branch of Fig. 36

Natural size

Perennial plants live for a series of years. Many kinds of trees last for centuries. The California giant redwoods, or *Sequoias* (Fig. 33), which reach a height of over 300 feet under favorable circumstances, live nearly 2000 years; and some enormous cypress trees found in Mexico were thought by Professor Asa Gray to be from 4000 to 5000 years old.

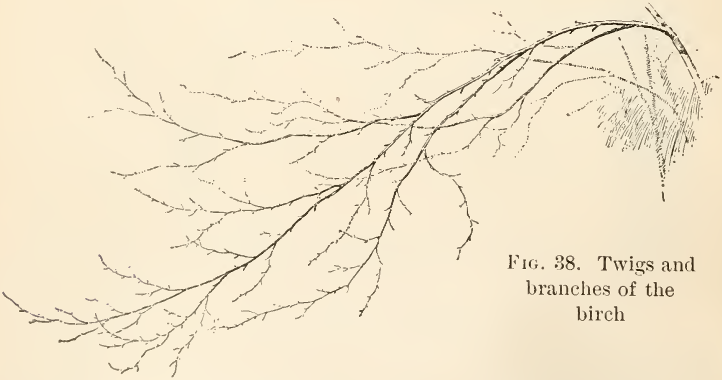

Fig. 38. Twigs and branches of the birch

Fig. 39. A Brazilian forest interior, with air plants and lianas

After Martius

61. Climbing and twining stems.[1] Since it is essential to the health and rapid growth of most plants that they should have free access to the sun and air, it is not strange that many should resort to special devices for lifting themselves above their neighbors. In tropical forests, where the darkness of the shade anywhere beneath the tree tops is so great that few flowering plants can thrive in it, the climbing plants, or *lianas* (Fig. 39), often run like great cables for hundreds of feet before they can emerge into the sunshine above. In temperate climates no such remarkable climbers are found, but many plants raise themselves for considerable distances. The principal means by which they accomplish this result are:

1. Producing roots at many points along the stem above ground and climbing on suitable objects by means of these, as in the English ivy (Fig. 14).
2. Laying hold of objects by means of tendrils or *twining branches* or *leaf-stalks,* as shown in Figs. 40 and 41.
3. Twining about any slender upright support, as shown in Fig. 42.
4. Clambering upon bushes and other supports by means of hooked prickles, as is done by some roses, blackberries, and cleavers (*Galium*).

FIG. 40. Coiling of a tendril of bryony

After Sachs

62. Tendril climbers. The plants which climb by means of tendrils are important subjects for study. Continued observation soon shows that the tips of tendrils sweep slowly about in a circular or oval course until they come in contact with some object around which they can coil. After the tendril has taken a few turns about its support, the free part of the tendril coils into a spiral and thus draws the whole stem toward the point

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[1] See Kerner and Oliver, *Natural History of Plants*, Vol. I, p. 669.

of attachment, as shown in Fig. 40. Some tendrils are modified leaves or stipules, as shown in Fig. 98; others are modified stems.

63. Irritability of tendrils. The coiling of tendrils is due to their irritability, aroused by the stimulus of contact with a solid object. After a latent period, varying with different species from a few seconds to more than an hour, the bending begins. It is caused either by contraction of the side in contact or by expansion of the opposite side; the exact mechanism of the process is not yet fully understood. The tendrils of the passion-flower plant will respond to the pressure of a bit of thread, hung on the tendril and kept in motion, whose weight is only a few millionths of a grain.

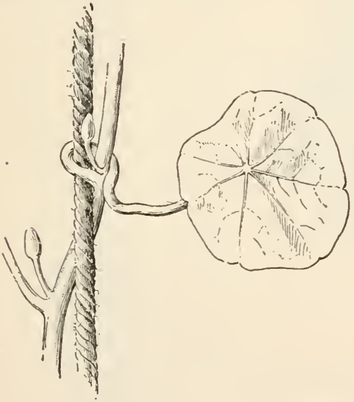

Fig. 41. Coiling of petiole of dwarf nasturtium (*Tropæolum*)

Fig. 42. Twining stem of hop After Decaisne

64. Twiners. Only a few of the upper internodes of the stem of a twiner are concerned in producing the movements of the tip of the stem. This is kept revolving in an elliptical or circular path until it encounters some roughish and not too stout object, about which it then proceeds to coil itself.

The movements of the younger internodes of the stems of twiners are among the most extensive of all the movements made by plants. A hop vine which has climbed to the top of its stake may sweep its tip continually around the circumference of a circle two feet in diameter, and the common wax plant (*Hoya*) of the greenhouses sometimes describes a five-foot circle, the tip moving at the rate of thirty-two inches per hour.[1] This circular motion is produced by unequal growth of the two sides of the stem.[2]

The direction in which twiners coil about a supporting object is almost always the same for each species of plant, but not the same for all species. In the hop it is as shown in Fig. 42, but in many plants the movement is in the reverse direction.

Fig. 43. The dandelion, a short-stemmed plant

65. Short-stemmed plants. As will be shown later (Chapter XXXIV), plants live subject to a very fierce competition among themselves, and they are exposed to almost constant attacks from animals.

While plants with long stems find it to their advantage to reach up as far as possible into the sunlight, the dandelion, the cinquefoil, the white clover, some spurges, the knotgrass, and hundreds of other species, living in open places, have found safety in hugging the ground. The dandelion, fall dandelion,

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[1] See article on "Climbing Plants," by Dr. W. J. Beal, in the *American Naturalist*, Vol. IV, pp. 405–415.

[2] See Strasburger, Noll, Schenk, and Schimper, *Text-Book of Botany*, pp. 257–260, New York, 1903.

shepherd's purse, and the like, with radiating leaves, are known as *rosette plants,* while those with radiating stems, like knotgrass, the clovers, and black medick (*Medicago*), are known as *mat plants.*

Fig. 45. Roots, rootstocks, and leaves of *Iris*

Fig. 44. Rootstock of cotton grass (*Eriophorum*)

Any plant which can grow in safety under the very feet of grazing animals will be especially likely to make its way in the world, since there are many places where it can flourish while ordinary plants would be destroyed. The bitter dandelion, which is almost uneatable for most animals on account of its taste, which lies too near the earth to be fed upon by grazing animals, and which bears being trodden on with impunity, is a type of a large class of hardy weeds.

The plants incorrectly called "stemless," like the dandelion (Fig. 43) and some violets, are not really stemless, but send out their leaves and flowers from a very short stem which hardly rises from the surface of the ground.

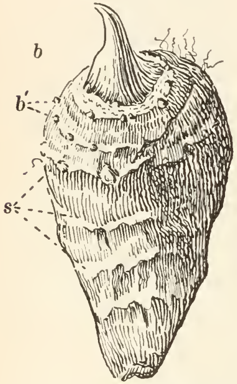

Fig. 46. Rootstock of caladium (*Colocasia*)

b, terminal bud; *b′*, buds arranged in circles where bases of leaves were attached; *s*, scars left by sheathing bases of leaves

Fig. 47. Part of a potato plant

The dark tuber in the middle is the one from which the plant has grown

66. Underground stems. Stems which lie mainly or wholly underground are of frequent occurrence and of many kinds. Some of the simplest kinds are called *rootstocks*. Familiar examples are those of some mints, of bloodroot, of Solomon's seal, and of many grasses, sedges, and ferns. The real nature of the creeping underground stem is frequently shown by the presence upon its surface of many scales, which are reduced leaves.

PLATE I. A sand-loving plant, sea rye grass

Rootstocks of this sort often extend horizontally for long distances in the case of grasses like the sea rye grass (Plate I), which roots itself firmly and thrives in shifting sand dunes. In the stouter rootstocks, like that of the iris (Fig. 45) and the caladium (Fig. 46), this stem-like character is less evident. The potato is an excellent example of the short and much-thickened underground stem known as a *tuber*.

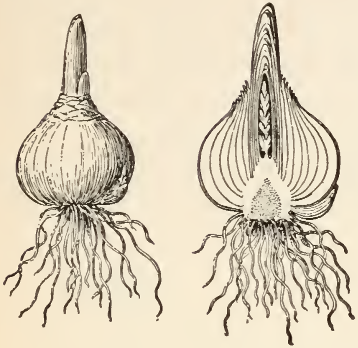

Fig. 48. Bulb of hyacinth

Exterior view, and split lengthwise.—After Faguet

It may be seen from Fig. 47 that the potatoes are none of them borne on true roots, but only on subterranean branches, which are stouter and more cylindrical than most of the roots. The "eyes" of the potato are rudimentary leaves and buds.

Fig. 49. Longitudinal section of an onion leaf

sca, thickened base of leaf, forming a bulb scale; *s*, thin sheath of leaf; *bl*, blade of the leaf; *int*, hollow interior of blade.—After Sachs

Bulbs, whether coated like those of the onion or the hyacinth (Fig. 48), or scaly like those of the lily, are merely very short and stout underground stems, covered with closely crowded scales or layers which represent leaves or the bases of leaves (Fig. 49).

The variously modified forms of underground stems just discussed illustrate in a marked way the storage of nourishment during the winter, or the rainless season, as the case may be, to provide the material for rapid growth during the active season. It is interesting to notice that a majority of the early flowering herbs in temperate climates, like the crocus, the snowdrop, the spring beauty, the tulip, and the skunk cabbage, owe their early blooming habit to richly stored underground stems of some kind, or to thick fleshy roots. Many of these very early blooming plants are woodland species which must hurry through most of the season's growth and begin to mature seed before the shade of the trees above them cuts off most of the necessary supply of light and before the drought of summer begins.

67. Condensed stems. The plants of desert regions require, above all, protection from the extreme dryness of the surrounding air, and usually from the excessive heat of the sun. Accordingly, many desert plants are found quite destitute of ordinary foliage, exposing to the air only a small surface. In the globular cactuses (Fig. 50) the stem appears reduced to the shape in which the least possible surface is presented by a plant of given bulk,--that is, in a somewhat spherical form. Other

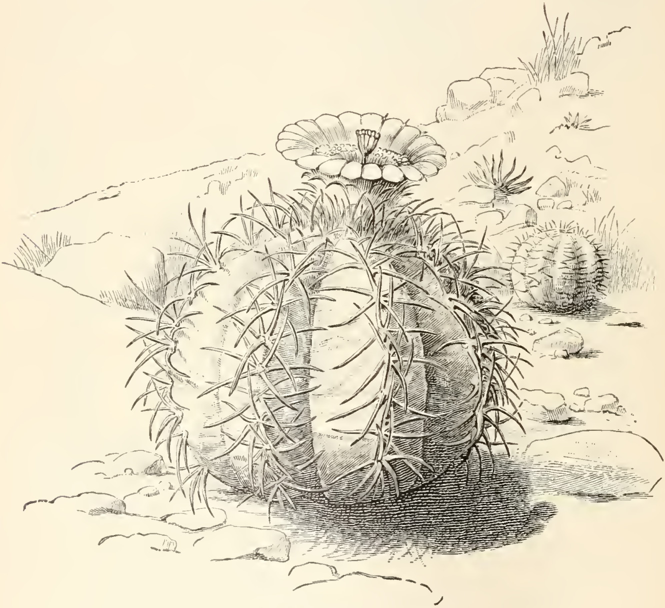

Fig. 50. A globular cactus

cactuses are cylindrical or prismatic, while still others consist of flattened joints; but all agree in offering much less area to the sun and air than is exposed by an ordinary leafy plant.

68. Leaf-like stems. The flattened stems of some kinds of cactus, especially the common showy *Phyllocactus*, are sufficiently like fleshy leaves, with their dark green color and imitation of a midrib, to pass for leaves. There are, however, a good many cases in which the stem takes on a more strikingly leaf-like form. The common asparagus sends up in spring shoots that bear large scales which are really reduced leaves. Later in the season, what seem like thread-like leaves cover the much-branched mature plant, but these green threads are actually minute branches, which perform the work of leaves (Fig. 51). The familiar greenhouse climber, wrongly known as smilax, properly called *Myrsiphyllum*, bears a profusion of what appear to be delicate green leaves (Fig. 52). Close study, however, shows that these are really short flattened branches, and that each little branch springs from the axil of a true leaf, *l*, in the form of a minute scale. Sometimes a flower and a leaf-like branch spring from the axil of the same scale.

FIG. 51. A spray of a common asparagus (not the edible species)

Branches which, like those of *Myrsiphyllum*, so closely resemble leaves as to be almost indistinguishable from them are called *cladophylls*, meaning branch leaves.

69. The range of modification of the stem. The stem may reach a length of many hundred feet, as in the tallest trees, in the great lianas of South American forests, or in the rattan of Indian jungles. On the other hand, in such plants as the primrose and the dandelion the stem may be reduced to a fraction of an inch in length. It may take on apparently root-like forms, as in many grasses and sedges, or become thickened by underground storage of starch and other plant food, as in the iris, the potato, and the crocus. Condensed forms of stem may exist above ground, or, on the other hand, branches may be flat and thin enough closely to imitate leaves. In short, the stem manifests great readiness in adapting itself to the most varied conditions of existence.

Fig. 52. Stem of *Myrsiphyllum*

l, scale-like leaves; *cl*, cladophyll, or leaf-like branch, growing in the axil of the leaf; *ped*, flower stalk, growing in the axil of a leaf

CHAPTER VII

STRUCTURE OF THE STEM

STEM OF MONOCOTYLEDONOUS PLANTS

70. External characters. The most familiar of the larger monocotyledonous plants are the grass-like ones, such as Indian corn, broom corn, and bamboo, the green briers (*Smilax*), and the palms. The stem of Indian corn consists of a series of smooth, slightly tapering internodes connected by enlarged nodes. Palm stems often have a very uneven surface, due to the projecting remains of old leafstalks (Fig. 53).

Fig. 53. Group of date palms

71. Internal structure. A cross section of a corn stem shows it to be composed of a hard, flinty rind, inclosing a very soft pith, which is traversed lengthwise by many slender fibers (Fig. 54). The fibers are arranged in a somewhat definite way, the smaller ones thickly clustered near the rind, the larger ones, less abundant, toward the center.

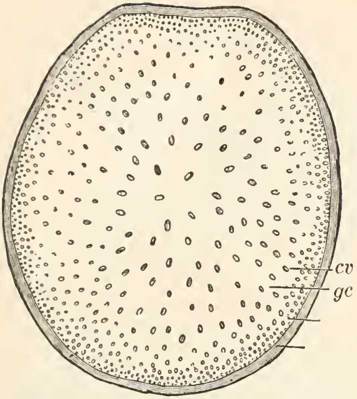

Fig. 54. Diagrammatic cross section of stem of Indian corn

cv, fibro-vascular bundles; *gc*, pithy material between bundles. — After Strasburger

In the bamboo, as in the cane of our southern canebrakes, the interior is hollow, with a hard, transverse partition at each node.

The fibers which traverse the pith of the corn stem are not solid cylinders, but are built up of cells of several kinds, around and between tubes, somewhat like those of Fig. 62. The whole structure is known as a *fibro-vascular bundle;* that is, a bundle of fibers and vessels, or tubes. In woody stems, such as those of the bamboo or palm, the bundles are closer together and much harder than in the corn stem. The outer rind of the latter is composed of long, thick-walled, slender cells, containing much silica and known as *sclerenchyma fibers.*

72. Mechanical function of the manner of distribution of material in monocotyledonous stems. The well-known strength and lightness of the straw of our smaller grains and of rods of cane or bamboo are due to their form. It can readily be shown by experiment that an iron or steel tube of moderate thickness, like a piece of gas pipe or of bicycle tubing, is much stiffer than a solid rod of the same weight per foot. The oat straw, the stems of bulrushes, the cane of our southern canebrakes, and the bamboo are hollow cylinders; the cornstalk is a solid cylinder, but filled with a very light pith. The flinty outer layer of the stalk, together with the closely packed sclerenchyma

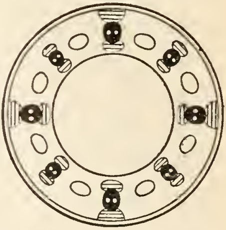

Fig. 55. Diagrammatic cross section of stem of bulrush (*Scirpus*), a hollow cylinder with strengthening fibers

After Kerner

fibers of the outer rind and the frequent fibro-vascular bundles just within this, are arranged in the best way to secure stiffness. In a general way, then, we may say that the pith, the bundles, and the sclerenchymatous rind are what they are and where they are to serve important mechanical purposes. But they have other uses fully as important (see Chapter VIII).

73. Growth of monocotyledonous stems in thickness. In most woody monocotyledonous stems, for a reason which will be explained later in this chapter, the increase in thickness is strictly limited. Such stems, therefore, as in many palms and in rattans, are less conical and more cylindrical than the trunks of ordinary trees, and are also more slender in proportion to their height.

STEM OF DICOTYLEDONOUS PLANTS

74. External characters. It is not easy to make any general statements about the external characters of dicotyledonous stems, on account of their very great variety of form. The student in his examination of twigs in connection with Chapter VI has learned a little about the appearance of a few woody stems. In general, the nodes are much less marked than in stems of corn, bamboo, and other grass-like forms. In the case of deciduous-leaved dicotyledonous plants, the scars left by fallen leaves are characteristic, quite unlike those mentioned in Sec. 70.

75. Internal structure.[1] If one begins his study of the structure of dicotyledonous stems with the one-year-old stem of a woody plant or with the stem of some such robust annual as hemp, sunflower, or the great ragweed, he will find it to be composed of a somewhat cylindrical pith, surrounded by a layer of wood usually of pretty even thickness, which is in its turn surrounded by a layer of bark (Fig. 56).[2]

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[1] For an account of the structure of the pine stem, see Sec. 352.

[2] Of course these layers are nearly cylindrical tubes, filled by pith or by wood and pith respectively. They are not of perfectly circular cross section, and they taper somewhat.

The wood cylinder may be discontinuous, that is, broken up into separate fibro-vascular bundles, as shown in Fig. 57; but even then the position of the wood between an inclosed pith

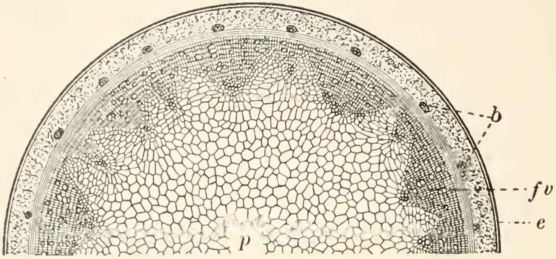

Fig. 56. Diagrammatic cross section of an annual dicotyledonous stem

p, pith; *fv*, woody or fibro-vascular bundles; *e*, epidermis; *b*, bundles of hard-bast fibers of the bark. Somewhat magnified. — After Frank

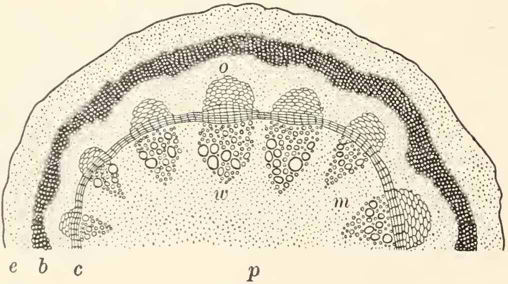

Fig. 57. Diagrammatic cross section of one-year-old *Aristolochia* stem

e, region of epidermis; *b*, hard-bast fibers; *o*, outer or bark part of a bundle; *w*, inner or woody part of bundle; *c*, cambium layer; *p*, region of pith; *m*, a medullary ray. Considerably magnified

The space between the hard bast and the bundles is occupied by thin-walled, somewhat cubical cells of the bark[1]

and an inclosing bark is notably different from the way in which the bundles are scattered in monocotyledonous stems.

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[1] In this and the following figure the relative prominence of the cambium layer is a good deal exaggerated.

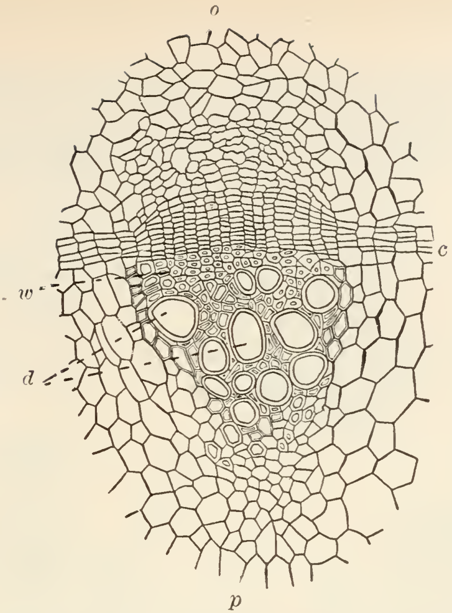

FIG. 58. One bundle from the preceding figure

w, wood cells; *d*, vessels. The other letters are as in Fig. 57. Many sieve cells occur in the region just outside of the cambium of the bundle. × 100

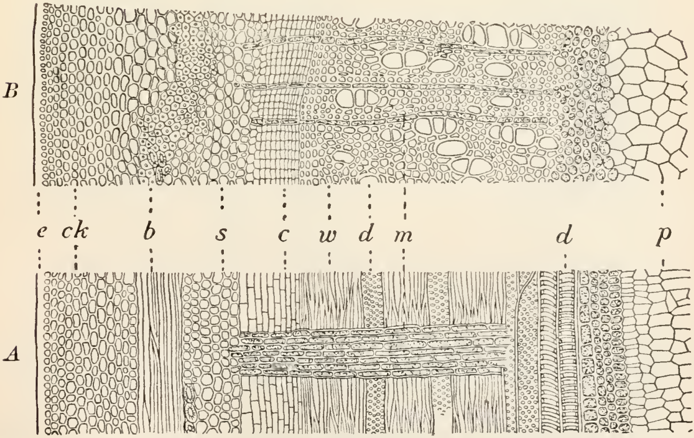

FIG. 59. Stem of box elder one year old

A, lengthwise (radial) section; *B*, cross section; *e*, epidermis; *ck*, cork; *b*, hard bast; *s*, sieve cells; *c*, cambium; *w*, wood cells; *m*, medullary rays; *d*, vessels; *p*, pith. Much magnified

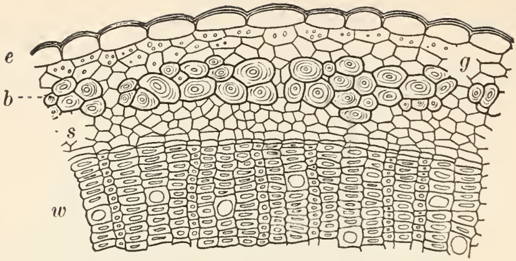

Fig. 60. Part of cross section of stem of flax

e, epidermis; *b*, hard bast; *s*, sieve cells; *w*, wood. Much magnified. — After Tschirch

Fig. 61

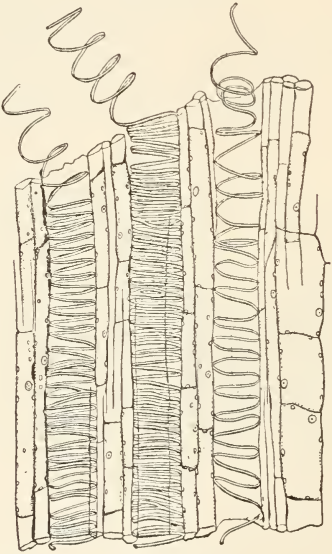

Fig. 62

Fig. 61. A group of hard-bast fibers

a, cut-off ends; *b*, lengthwise section of fibers. Greatly magnified. — After Tschirch

Fig. 62. A lengthwise section of a group of spiral vessels from the stem of sunflower

At the top of the figure some of the spiral threads which line the vessels are seen partly uncoiled. Greatly magnified. — After Frank

76. Disposition of material for strengthening purposes. Only two of the many ways in which the stem is strengthened need be mentioned here. In a majority of cases it owes its stiffness mainly to the wood, as shown in Fig. 56. But not infrequently most of the stiffening material consists of the *hard-bast* fibers found in the bark. It is this layer in flax (Fig. 60) which is utilized in the manufacture of linen thread and linen fabrics.

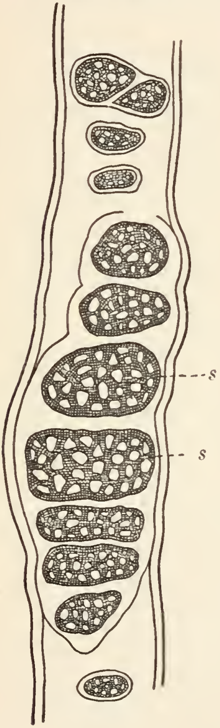

Fig. 63

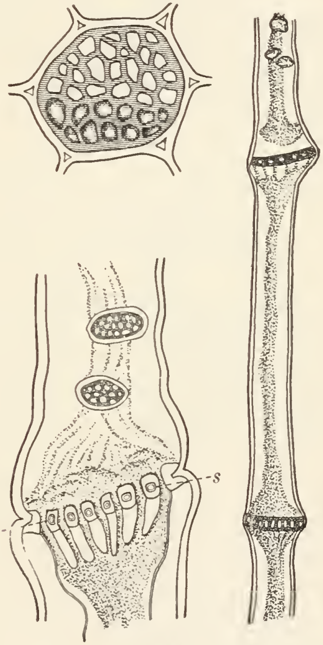

Fig. 64

Fig. 63. Part of a sieve tube from linden

s, sieve plates on the cell wall. × about 900. — After Thomé

Fig. 64. Parts of sieve tubes as found in plants of the gourd family

ss, a sieve plate seen edgewise; above it a similar one, surface view. Greatly magnified. — After Thomé

77. Structural units of the dicotyledonous stem. The student should already, from his own examinations, have learned a good deal about the kinds of cells and cell aggregates which compose the stem. The preceding figures (Figs. 56–60) will serve to illustrate the most important of these, and Figs. 61–64 show some of them more in detail.

78. Parenchyma, prosenchyma, and collenchyma. A mass of similar coöperating cells is called a *tissue*.[1] Two of the principal classes not previously mentioned which occur in the stem are *parenchymatous* tissue and *prosenchymatous* tissue. *Parenchyma* is well illustrated by the green layer of the bark, by wood parenchyma, and by pith. Its cells are usually somewhat roundish or cubical, at any rate not many times longer than wide, and at first rather full of protoplasm. Their walls are not generally very thick. *Prosenchyma*, illustrated by hard bast and masses of wood cells, consists of thick-walled cells many times longer than wide, containing little protoplasm and often having little or no cell cavity.

As a rule the stems of the most highly developed plants owe their toughness and their stiffness mainly to prosenchymatous tissue. In some stems, particularly the fleshy ones, the stiffness is, however, largely due to *collenchyma*, a kind of parenchyma in which the cells are thickened or reënforced at their angles, as shown in Fig. 65.

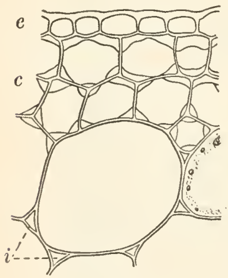

Fig. 65. Collenchymatous and other tissue from stem of balsam (*Impatiens*)

e, epidermis; *c*, collenchyma; *i*, intercellular spaces between large parenchyma cells.—After Strasburger

79. The early history of the stem. In the earliest stages of the growth of the stem it consists entirely of thin-walled and rapidly dividing cells. Soon, however, the various kinds of tissue which are found in the full-grown stem begin to appear.

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[1] See Strasburger, Noll, Schenck, and Schimper, *Text-Book of Botany*, pp. 92–95, 2d ed., London, 1903.

In Fig. 66 the process is shown as it occurs in the castor bean. At *m,* in *B,* is the central column of pith surrounded by eight fibro-vascular bundles, *fv,* each of which contains a number of vessels arranged in a somewhat regular manner and surrounded by the forerunners of the true wood cells.

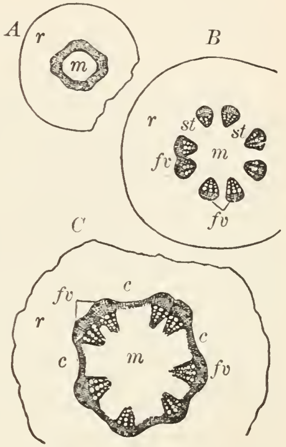

Fig. 66. Transverse section through the hypocotyl of the castor-oil plant at various stages

A, after the root has just appeared outside the testa of the seed; *B*, after the hypocotyl is nearly an inch long; *C*, at the end of germination; *r*, cortex (undeveloped bark); *m*, pith; *st*, medullary rays; *fv*, fibro-vascular bundles; *c*, layer of tissue which is to develop into cambium. Considerably magnified. — After Sachs

In *C* the section shows a considerable advance in growth: the fibro-vascular bundles are larger and are now connected by a rapidly growing layer of tissue *c*.

As growth continues, this layer becomes the *cambium layer,* composed of thin-walled and rapidly dividing cells, as shown in Figs. 67 and 68.

80. Secondary growth. From the inside of the cambium layer the wood cells and ducts of the mature stem are produced, while from its outer circumference the new layers of the bark proceed. From this mode of increase the stems of dicotyledonous plants are called *exogenous,* that is, outside growing. The presence of the cambium layer on the outside of the wood in early spring is a fact well known to the schoolboy who pounds the cylinder cut from an alder, willow, or hickory branch until the bark will slip off and so enable him to make a whistle. The sweet taste of this pulpy layer, as found in the white pine, the slippery elm, and the basswood, is a familiar evidence of the nourishment which the cambium layer contains. It is also, as might be supposed, very rich in proteids.

With the increase of the fibro-vascular bundles of the wood, the space between them, at first large, becomes less, and the pith, which extended freely out toward the bark, becomes compressed into thin plates so as to form medullary rays.

These are, as already stated, of value in storing the food which the plant in cold and temperate climates lays up in the summer and fall for use in the following spring, and in the very young stem they serve as an important channel for the transference of fluids across the stem from bark to pith, or in the reverse direction. On account, perhaps, of their importance to the plants, the cells of the medullary rays are among the longest lived of all vegetable cells, retaining their vitality in the beech tree sometimes, it is said, for more than a hundred years.

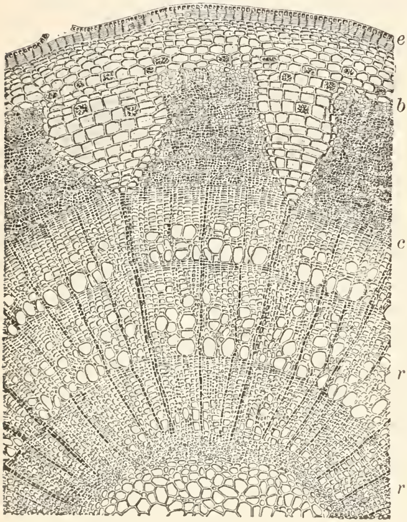

Fig. 67. Cross section of a three-year-old linden twig

e, epidermis and corky layer of the bark; *b*, bast; *c*, cambium layer; *r*, annual rings of wood. Much magnified. — After Kny

After the interspaces between the first fibro-vascular bundles have become filled up with wood, the subsequent growth must take place in the manner shown in Fig. 68. The cambium of the original wedges of wood *fc*, and the cambium *ic* formed between these wedges, continues to grow from the inner and from the outer surface, and thus causes a permanent increase in the diameter of the stem and a thickening of the bark, which, however, usually soon begins to peel off from the outside and thus remains pretty constant in thickness.

It is the lack of any such ring of cambium as is found in dicotyledonous plants, or even of permanent cambium in the separate bundles, that makes it impossible for the trunks of most palm trees to grow indefinitely in thickness, like that of an oak or an elm.

81. Stem structure of climbing shrubs. Some of the most remarkable kinds of dicotyledonous stems are found in climbing shrubs. The bundles, as shown in Fig. 57, are much more distinct than in most other woody stems. It is evident that this is for the sake of leaving the stem flexible for twining purposes, just as a wire cable is adapted to be wound about posts or other supports, while a solid steel or iron rod of the same size would be too stiff for this use.

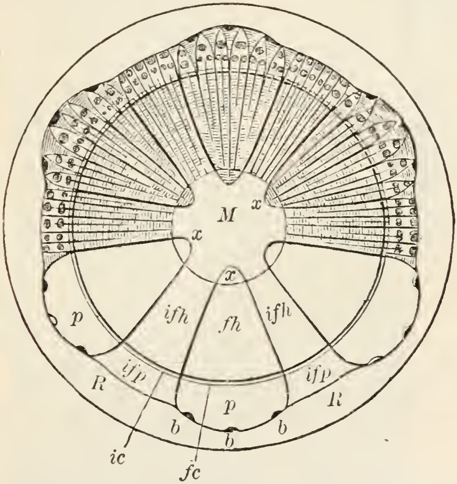

FIG. 68. Diagram to illustrate secondary growth in a dicotyledonous stem

R, the first-formed bark; *p*, mass of sieve cells; *ifp*, mass of sieve cells between the original wedges of wood; *fc*, cambium of wedges of wood; *ic*, cambium between wedges; *b*, groups of bast cells; *fh*, wood of the original wedges; *ifh*, wood formed between wedges; *x*, earliest wood formed; *M*, pith. — After Sachs

82. Interruption of annual rings by branches; knots. When a leaf bud is formed on the trunk or branch of a dicotyledonous tree it is connected with the wood by fibro-vascular bundles.

As the bud develops into a branch, the few bundles which it originally possessed increase greatly in number, and at length, as the branch grows, form a cylinder of wood which cuts across the annual rings, as shown in Fig. 69. This interruption to the rings is a knot, such as one often sees in boards and planks. If the branch dies long before the tree does, the knot may be buried under many rings of wood. What is known as "clear" lumber is obtained from trees that have grown in a dense forest, so that the lower branches of the larger trees were killed by the shade many years before the tree was felled.

In pruning fruit trees or shade trees the branches which are removed should be cut close to the trunk. If this is done, the growth of the trunk will bury the scar before decay sets in.

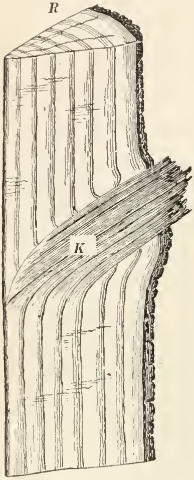

Fig. 69. Formation of a knot in a tree trunk

R, cut-off end of stick, showing annual rings; *K*, knot formed by growth of a branch. — After Roth

Fig. 70. Grafting

At the left scion and stock are shown ready to be united; at the right they are joined and ready to cover with grafting wax. — After Percival

83. Grafting. When the cambium layer of any vigorously growing stem is brought in contact with the same layer in another stem of the same kind or a closely similar kind of plant, the two may grow together to form a single stem or branch. This process is called *grafting*, and is much resorted to in order to secure apples, pears, etc., of any desired kind (Fig. 70). A twig known as the *scion* from a plant of the chosen variety may be grafted upon another individual *of similar kind* known as the *stock*, and the resulting stems will bear the wished-for sort of fruit. Often one species is grafted on another, as the pear on the quince or the apple. Rarely trees differing as much as the chestnut and the oak may be grafted together.

FIG. 71. Two ash trees naturally grafted together

After Werthner

Sometimes grafting comes about naturally by the branches of a tree chafing against one another until the bark is worn away and the cambium layer of each is in contact with that of the other, or two separate trees may be joined by natural grafting into a nearly cylindrical double trunk, as is shown in Fig. 71.

84. Comparison of the monocotyledonous and the dicotyledonous stem.[1]

	Monocotyledonous Stem	Dicotyledonous Stem
General Structure :	A hard rind of rather uniform structure. Bundles intermixed with the pith.	A complex bark, usually on young shoots, consisting of an epidermis, a corky layer, a green layer, and a layer of bast. A layer of cambium. Wood in annual rings. Pith in a cylinder at the center.
Structure of Bundles :	Bundles *closed*; that is, without permanent cambium.	Bundles *open*, with permanent cambium.
Growth in Thickness :	Cells of mature parts of stem expand somewhat, but (in most palms) new ones are not formed.	New wood cells formed throughout growing season from cambium ring.

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[1] This comparison applies only to most of the woody or tree-like stems.

CHAPTER VIII

LIVING PARTS OF THE STEM; WORK OF THE STEM

85. Active portions of the stems of trees and shrubs. In annual plants generally, and in the very young shoots of shrubs and trees, there are *stomata* (singular *stoma*, meaning mouth), or breathing pores, which occur abundantly in the epidermis, serving for the admission of air and the escape of moisture, while the green layer of the bark answers the same purpose that is served by the green pulp of the leaf (Chapter XII). For years, too, the spongy *lenticels*, which succeed the stomata and occur scattered over the external surface of the bark of trees and shrubs, serve to admit air to the interior of the stem. The lenticels at first appear as roundish spots, of very small size; but as the twig or shoot on which they occur increases in diameter, the lenticel becomes spread out at right angles to the length of the stem, so that it sometimes becomes a longer transverse slit or scar on the bark, as in the cherry and the birch and the elder. But in the trunk of a large tree often no part of the bark except the inner layer is alive. The older portions of the bark, such as the highly developed cork of the cork oak, sometimes cling for years after they are dead and useless except as a protection for the parts beneath against mechanical injuries or against cold. But in many cases, as in the shellbark hickory and the grapevine, the old bark soon falls off in strips; or as in birches it finally peels off in bands around the stem.

The cambium layer is very much alive, and so is the young outer portion of the wood. Testing this sapwood, particularly in winter, shows that it is rich in starch and proteids.

The heartwood of a full-grown tree is hardly living, unless the cells of the medullary rays retain their vitality, and so it is probable that wood of this kind is chiefly useful to the tree by giving stiffness to the trunk and larger branches, thus preventing them from being easily broken by storms.

It is therefore possible for a tree to flourish, sometimes for centuries, after the heartwood has much of it rotted away and left the interior of the trunk hollow, as shown in Fig. 72.

86. Uses of the components of the stem. There is a marked division of labor among the various groups of cells that make up the stem of ordinary dicotyledons, particularly in the stems of trees, and it will be best to explain the uses of the kinds of cells as found in trees rather than in herbaceous plants. A few of the ascertained uses of the various tissues are these:

The *pith* forms a large part of the bulk of very young shoots, since it is a part of the tissue of comparatively simple structure amid which the fibro-vascular bundles arise. In mature stems it becomes rather unimportant, though it often continues for a long time to act as a storehouse of food.

The *medullary rays* in the young shoot serve as a channel for the transference of water and plant food in a liquid form across the stem, and they often contain much stored food.

The *vessels* carry water upward through the stem in certain plants.

The *wood cells of the heartwood* are useful only to give stiffness to the stem. Those of the sapwood, in addition to this work, have to carry most of the water from the roots to the leaves and other distant portions of the plant.

The *cambium layer* is the region in which the annual growth of the tree takes place.

Sieve tubes form the most important portion of the inner bark, carrying elaborated plant food from the leaves toward the roots.

The *green layer of the bark* in young shoots does much toward collecting nutrient substances, or raw materials, and preparing the food of the plant from air and water, but this work may be best explained in connection with the study of the leaf (Chapter XII).

FIG. 72. Pioneer's cabin, a hollow giant redwood (*Sequoia*)

After White

87. Movement of water in the stem. The student has already learned that large quantities of water are taken up by the roots of plants.

Having become somewhat acquainted with the structure of the stem, he is now in a position to investigate the question how the various fluids, commonly known as sap, travel about in it.[1] It is important to notice that sap is by no means the same substance everywhere and at all times. As it first makes its way by osmotic action inward through the root hairs of the growing plant it differs but little from ordinary spring water or well water. The liquid which flows from the cut stem of a "bleeding" tree or grapevine which has been pruned just before the buds have begun to burst in the spring is mainly water, often with a little dissolved organic acids, proteids, and sugar. The sap which is obtained from maple trees in late winter or early spring, and is boiled down for sirup or sugar, is richer in nutritious material than the water of the grapevine, while the elaborated sap which is sent so abundantly into the ear of corn at its period of filling out, or into the growing pods of beans and peas, or into the rapidly forming acorn or the chestnut, contains great stores of food suited to sustain plant or animal life.

FIG. 73. Channels for the movement of water, upward and downward

The heavy black lines in roots, stems, and leaves show the course of the fibro-vascular bundles through which the principal movements of water take place. — After Frank and Tschirch

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[1] See the paper on "The So-called Sap of Trees and its Movements," by Professor Charles R. Barnes, *Science*, Vol. XXI, p. 535.

From the familiar facts that ordinary forest trees apparently flourish as well after the almost complete decay and removal of their heartwood, and that many kinds will live and grow for a considerable time after a ring of bark extending all round the trunk has been removed, it may readily be inferred that the crude sap in trees must rise through some portion of the newer layers of the wood. A tree girdled by the removal of a ring of sapwood promptly dies. After the removal of a ring of bark a tree dies from starvation of the roots (Sec. 88; also see Fig. 394).

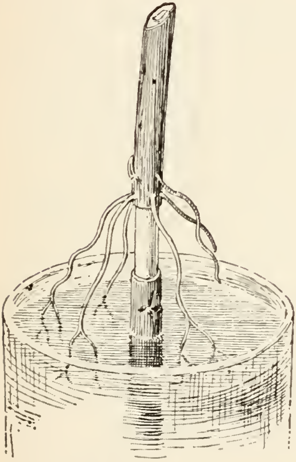

Fig. 74. A cutting girdled and sending down roots from the upper edge of the girdled ring

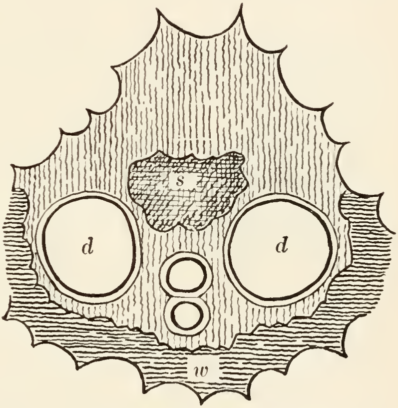

Fig. 75. Diagrammatic cross section of a bundle from sugar cane, showing channels for water and dissolved plant food

Water travels upward through the vessels *d* and through the wood cells in the region marked *w*. Water with dissolved plant food travels downward through the sieve tubes in the region *s*. Magnified

88. Downward movement of liquids. Most dicotyledonous stems, when stripped of a ring of bark and then set in water, as shown in Fig. 74, and covered with a bell jar, develop roots only at or near the upper edge of the stripped portion. This would seem to prove that such stems send their building material — the elaborated sap — largely, at any rate, down through the bark. Its course is undoubtedly for the most part through the sieve tubes (Figs. 63, 64), which are admirably adapted to convey liquids. In addition to these general upward and downward movements of sap, there must be local transfers laterally through the stem, and these are at times of much importance to the plant.

Since the liquid building material travels straight down the stem, that side of the stem on which the manufacture of such material is going on most rapidly should grow fastest. Plant food is made out of the raw materials by the leaves, and so the more leafy side of a tree forms thicker rings than the less leafy side, as shown in Fig. 76.

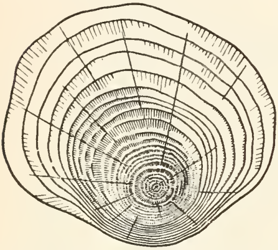
Fig. 76. Unequal growth of rings of wood in a nearly horizontal stem of juniper

Natural size

89. Rate of movement of water in the stem. There are many practical difficulties in the way of ascertaining exactly how fast the watery sap travels from the root to the leaves. It is, however, easy to illustrate experimentally the fact that it does rise, and to give an approximate idea of the time required for its ascent. The best experiment for beginners is one which deals with an entire plant under natural conditions; that is, by allowing a plant to wilt from lack of water, then watering it freely and noting how soon the leaves begin to recover their natural appearance and positions.

The interval of time will give a very rough idea of the time of transfer of water through the roots and the stem of the plant. From this, by measuring the approximate distance traveled, a calculation could be made of the number of inches per minute that water travels in this particular kind of plant, through a route which is partly roots, partly stem, and partly petiole. Still another method is to immerse the cut ends of leafy stems in eosin solution and note carefully the rate of ascent of the coloring liquid. This plan is likely to give results that are too low; still it is of some use. It has given results varying from 34 inches per hour for the willow to 880 inches per hour for the sunflower. A better method is to introduce the roots of the plant which is being experimented upon into a weak solution of some chemical substance which is harmless to the plant and which can readily be detected anywhere in the tissues of the plant by chemical tests. Proper tests are then applied to portions of the stem which are cut from the plant at short intervals of time.

Compounds of the metal lithium are well adapted for use in this mode of experimentation, if a spectroscope is available to test for its presence.

90. Causes of movements of water in the stem. Some of the phenomena of osmosis were explained in Secs. 48–51, and the work of the root hairs was described as due to osmotic action.

That portion of the sap pressure which originates in the roots (Sec. 38), being apparently able to sustain a column of water only 80 or 90 feet high at the most (and usually less than half this amount), would be quite insufficient to raise the sap to the tops of the tallest trees, since many kinds grow to a height of more than 100 feet. Our California "big trees," or *Sequoias*, reach the height of over 300 feet, and an Australian species of Eucalyptus, it is said, sometimes towers up to 470 feet. Root pressure, then, may serve to start the soil water on its upward journey, but some other force or forces must step in to carry it the rest of the way. What these other forces are is still a matter of discussion among botanists.

The slower inward and downward movement of the sap may be explained as due to osmosis. For instance, in the case of growing wood cells, sugary sap descending from the leaves into the stem gives up part of its sugar to form the cellulose of which the wood cells are being made.

This loss of sugar leaves the sap rather more watery than usual, and osmosis carries it from the growing wood to the leaves, while at the same time a slow transfer of the dissolved sugar is set up from leaves to wood. The water is thrown off in the form of vapor as fast as it reaches the leaves, so that they do not become distended with water, while the sugar is changed into cellulose and built into new wood cells as fast as it reaches the region where such cells are being formed.

Plants in general[1] readily change starch to sugar, and sugar to starch. When they are depositing starch in any part of the root or stem for future use, the withdrawal of sugar from those portions of the sap which contain it most abundantly gives rise to a slow movement of dissolved particles of sugar in the direction of the region where starch is being laid up.

91. Storage of food in the stem. The reason why the plant may profit by laying up a food supply somewhere inside its tissues has already been suggested (Sec. 33).

The most remarkable instance of storage of food in the stem is probably that of sago palms, which contain an enormous amount, sometimes as much as eight hundred pounds, of starchy material in a single trunk. But the commoner plants of temperate regions furnish abundant examples of deposits of food in the stem.

92. Storage in underground stems. The branches and trunk of a tree furnish the most convenient place in which to deposit food during winter to begin the growth of the following spring. But in those plants which die down to the ground at the beginning of winter the storage must be either in the roots or in underground portions of the stem.

Rootstocks, tubers, and bulbs seem to have been developed by plants to answer as storehouses through the winter (or in some countries through the dry season) for the reserve materials which the plant has accumulated during the growing season. The commonest tuber is the potato, and this fact and the points of interest which it represents make it especially desirable to use for a study of the underground stem in a form most highly specialized for the storage of starch and other valuable products.

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[1] Not including most of the spore plants.

It is evident that in the potato we have to do with a very highly modified form of stem. The corky layer of the bark is well represented, and the loose cellular layer beneath is much developed; wood is almost lacking, but the pith is greatly developed and constitutes the principal bulk of the tuber. All this is readily understood if we consider that the tuber, buried in and supported by the earth, does not need the kinds of tissue which give strength, but only those which are well adapted to store the requisite amount of food.

93. Occurrence of sugar in the stem. *Grape sugar* is an important substance among those used for food by the plant. It received its name from the fact that it was formerly obtained for chemical examination from grapes. Old dry raisins usually show little masses of whitish material scattered over the skin which are nearly pure grape sugar. Commercially it is now manufactured on an enormous scale from starch by boiling with diluted sulphuric acid. In the plant it is made from starch by processes as yet imperfectly understood, and another sugar, called *maltose*, is made from starch in the seed during germination. Sugar is not as well adapted for reserve deposits as starch, since it ferments easily and may escape by osmosis from tissues which contain it. In the onion bulb it is stored in considerable quantities and may be detected by a simple chemical test.

CHAPTER IX

BUDS

94. Structure of winter buds. Dissection of most winter buds shows that they are composed of an outer covering of tough, often hairy or resin-covered scales and an interior mass of small undeveloped leaves, closely packed together. Not infrequently a rudimentary flower cluster occupies the central portion of the bud.

Fig. 77. Dissected bud of buckeye (*Æsculus macrostachya*), showing transitions from bud scales to leaves

95. Nature of bud scales. The fact that the bud scales are in certain cases merely imperfectly developed leaves or leafstalks is often clearly manifest from the series of steps connecting the bud scale on the one hand with the young leaf on the other, which may be found in many opening buds, as illustrated by Fig. 77. In other buds the scales are not imperfect leaves, but the little appendages (*stipules,* Figs. 89, 90) which occur at the bases of leaves. This kind of bud scale is especially well shown in the magnolia and the tulip tree and in the familiar "rubber plant" (*Ficus elastica*).

96. Naked buds. All the kinds above mentioned are *resting buds,* and in temperate or cold climates *winter buds,* capable of

Fig. 79. Alternate leaves of cultivated cherry, with buds in their axils, in October

living through the colder months of the year, and are also *scaly* buds.

In the herbs of temperate climates, and even in shrubs and trees of tropical regions, the buds are often *naked;* that is, nearly or quite destitute of scaly coverings (Fig. 78). These are best suited for a season or a climate which is both warm and moist. The scales, of whatever sort, with their coatings of hair or of resinous material, are of use mainly in protecting buds from sudden changes of temperature or too rapid loss of water. The latter, in climates like that of southern California or the Mediterranean coast, would be during the rainless summer.

Fig. 78

Tip of branch of *Ailanthus* in winter condition, showing very large leaf scars and nearly naked buds

In most cold or temperate climes it would be during the winter, when little water can be drawn from the soil (Sec. 39).

97. Position of buds. The distinction between *lateral* and *terminal* buds has already been alluded to (Sec. 57).

The plumule is the first terminal bud which the plant produces. Lateral buds are usually *axillary*, as shown in Fig. 79, that is they grow in the angle formed by the leaf with the stem (Latin, *axilla*, armpit); but not infrequently there are several buds grouped in some way about a single leaf axil, either one above the other, as in the butternut (Fig. 80), or grouped side by side, as in the red maple, the cherry, and the box elder (Fig. 81).

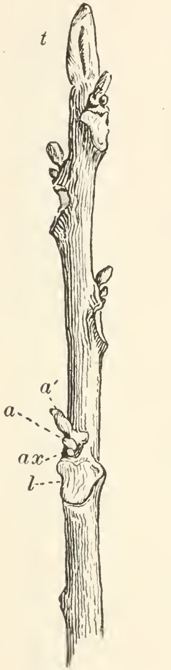

Fig. 80. Accessory buds of butternut

l, leaf scar; *ax*, axillary bud; *a*, *a′*, accessory buds; *t*, terminal bud. Reduced.

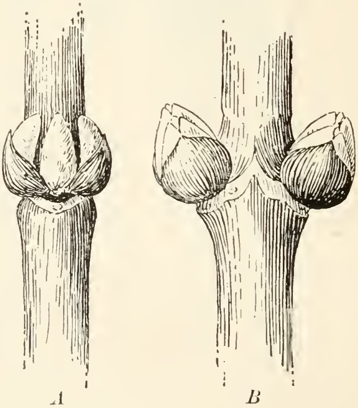

Fig. 81. Accessory buds of box elder (*Negundo*)

A, front view of group; *B*, two groups seen in profile. Magnified

In these cases all the buds, except the axillary one, are called *accessory* or *supernumerary* buds. Those which appear in irregular positions, as on roots, on unusual parts of the stem, or on leaves (Fig. 88), are called *adventitious buds.*

98. Leaf buds and flower buds; the bud an undeveloped branch. Buds are of three principal classes: *leaf buds,* in which the parts inside of the scales develop into leaves, and their central axes into stems; *mixed buds,* which contain both leaves and flowers in an undeveloped condition; and *flower buds,* which contain the rudiments of flowers only.

Sometimes, as in the black walnut and the butternut, the leaf buds and flower buds are readily distinguishable by their difference in form; while in other cases, as in the cultivated cherry, the difference in form is but slight. In many plants, as the lilac, there is a notable difference in size.

FIG. 82

A, a pear leaf bud in autumn; *B*, a leafy shoot derived from *A*, as seen in the middle of the following summer, with flower bud at tip; *C*, the fruit spur, *B*, in autumn, after the fall of the leaves. — After Percival

The rings of scars about the twig, shown in Figs. 79 and 84, mark the place where the bases of bud scales were attached. A little examination of the part of the twig which lies above this ring, as shown in Fig. 79, will lead one to the conclusion that this portion has all grown in the one spring and summer since the bud scales of that particular ring dropped off.

Following out this suggestion, it is easy to reckon the age of any moderately old portion of a branch, since it is equal to the

Fig. 83. Fruit bud of pear (same as *C*, of Fig. 82), showing its development

A, opening in spring; *B*, later, developing flowers and leaves; *C*, later still: only one flower has produced a fruit, the rest having fallen off. Below it is a lateral bud which will continue the spur next year. — After Percival

number of segments between the rings. In rapidly growing shoots of willow, poplar, and similar trees, five or ten feet may be the growth of a single year, while in the lateral twigs of the hickory, apple, or cherry, the yearly increase may be but a fraction of an inch. Such "spurs" as are shown in Figs. 82–84 are of little use in the permanent growth of the tree, and poplars, elms, soft maples, and other trees shed the oldest of these every year. In any case the growth is but the development of the bud, which may be regarded as an undeveloped stem or branch, with its internodes so shortened that successive leaves seem almost to spring from the same point.

Fig. 84. A slowly grown twig of cherry, three inches long and about ten years old

The pointed bud *l* is a leaf bud; the more obtuse accessory buds *f*, *f* are flower buds

99. Vernation. The arrangement of leaves in the bud is called *vernation;* some of the principal modes are shown in Fig. 86. In the cherry the two halves of the leaf are folded together flat, with the under surfaces outward; in the walnut the separate *leaflets,* or parts of the leaf, are folded flat and then grouped into a sort of cone; in the snowball each half of the leaf is plaited in a somewhat fan-like manner, and the edges of the two halves are then brought round so as to meet; in the lady's mantle the fan-like plaiting is very distinct; in the wood sorrel each leaflet is folded smoothly, and then the three leaflets packed closely side by side. All these modes of vernation, and many others, often characteristic of groups of plants, have received descriptive names by which they are known to botanists.

100. Importance of vernation. The significance of vernation is best understood by considering that there are two important purposes to be served: the leaves must be stowed as closely as possible in the bud, and upon beginning to open they must be protected from too great heat and dryness until they have reached a certain degree of firmness. It may be inferred from Fig. 86 that it is common for very young leaves to stand vertically. This protects them considerably from the scorching effect of the sun at the hottest part of the day. Many young leaves, as, for instance, those of the silver-leafed poplar, the pear, the beech, and the mountain ash, are sheltered and protected from cold, dryness, and the attacks of small

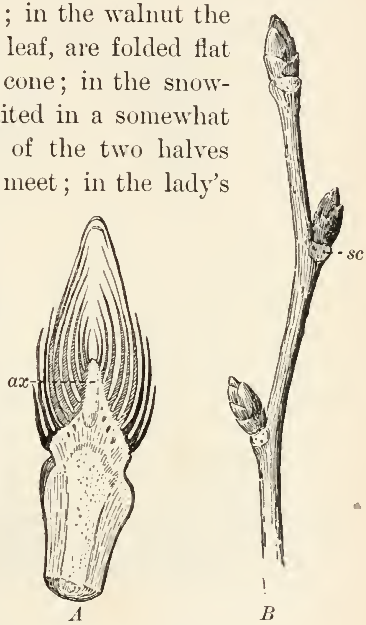

Fig. 85

B, a twig of European elm; *A*, a longitudinal section of the buds of *B* (considerably magnified); *ax*, the axis of the bud, which will elongate into a shoot; *sc*, leaf scars. — After Behrens insects by a coating of wool or down, which they afterwards lose. The leaves of the tulip tree are inclosed for a little time

Fig. 86. Types of vernation

1, 2, cherry; 3, 4, European walnut; 5, 6, snowball; 7, lady's mantle; 8, oxalis. After Kerner

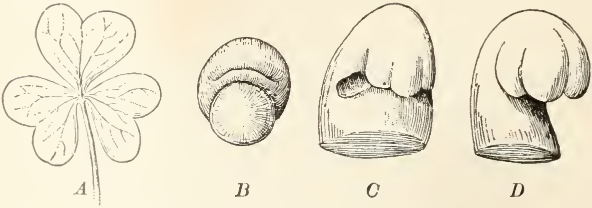

Fig. 87. Development of an oxalis leaf

A, full-grown leaf; *B*, rudimentary leaf, the leaflets not yet evident; *C*, more advanced stage, the leaflets appearing; *D*, a still more advanced stage. *B*, *C*, and *D*, considerably magnified. — After Frank in thin pouches, which serve as bud scales, and are thus entirely shielded from direct contact with the outside air.

101. Dormant buds. Generally some of the buds on a branch remain undeveloped in the spring, when the other buds are beginning to grow, and this inactive condition may last for many seasons. Finally the bud may die, or some injury to the tree may destroy so many other buds as to leave the dormant ones an extra supply of food, and this, with other causes, may force them to develop and to grow into branches.

Sometimes the tree altogether fails to produce buds at places where they would regularly occur. In the lilac the terminal bud usually fails to appear, and the result is constant forking of the branches.

102. Adventitious buds. Buds which occur in irregular places, that is, not terminal nor in or near the axils of leaves, are called *adventitious buds;* they may spring from the roots, as in the silver-leafed poplar, or from the sides of the trunk, as in our American elm. In many trees, for instance willows and maples, they are sure to appear after the trees have been cut back. Willows are thus cut back, or *pollarded,* in order to cause them to produce a large crop of slender twigs suitable for basket making.

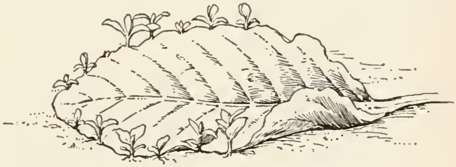

Fig. 88. Budding leaf of *Bryophyllum*

Leaves rarely produce buds, but a few kinds do so when they are injured. Those of the *Bryophyllum* (Fig. 88), a plant allied to the garden live-forever, when they are removed from the plant while they are still green and fresh, almost always send out buds from the margin. These do not appear at random, but are borne at the notches in the leaf margin and are accompanied almost from the first by minute roots. This plant seems to rely largely upon leaf budding to reproduce itself, for in a cool climate it rarely flowers or seeds.

CHAPTER X

LEAVES

103. The leaf as a member of the plant body. Among seed plants the plant body consists of root and shoot. The latter is made up of stem and leaves. It is difficult to frame a simple and exact definition for the leaf, but every one is sufficiently familiar with the appearance of the ordinary foliage leaves of plants, and there is no difficulty in identifying these. The unusual scale-like, bristle-shaped, tendril-shaped, or pitcher-form leaves are often hard to recognize as such.

Fig. 89. Leaf of apple, with stipules

After Thomé

104. Parts of the leaf. In the typical foliage leaf there are three parts, — the expanded portion, or *blade* (lamina), the *leafstalk* (petiole), and a pair of appendages at the base of the petiole known as *stipules.* Many leaves have no petiole and are said to be *sessile* (meaning sitting). Others have no blade and perform their functions as foliage by means of a flattened petiole or large stipules. Most leaves are *bilaterally symmetrical ;* that is, they have a right and a left half, which, if folded together along the middle line of the leaf, would nearly coincide. Usually the upper and the under surface differ from each other in color, smoothness, and other respects.

Fig. 90. Leaf of pansy, with leaf-like stipules

After Decaisne

105. Veining. The blade of the leaf is traversed by a framework of fibro-vascular bundles known as *veins.* These are arranged in many ways, but the two principal types are *closed,* or *parallel-veined,* and *open,* or *netted-veined,* leaves. In the former the veins run more or less nearly parallel, either from base to tip of the leaf, or from a midrib outward. In the latter the veins are branched so as to form a network.

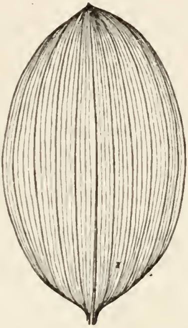

FIG. 91. Parallel-veined leaf of Solomon's seal

After Strasburger

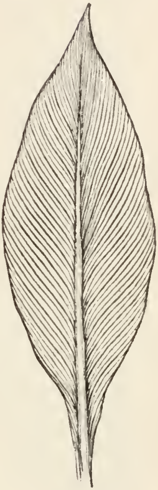

FIG. 92. Parallel veining in canna. Veins running from midrib to margin

106. Palmate and pinnate veining. In netted-veined leaves several ribs may radiate from the end of the petiole, like the sticks of a fan. Such veining is said to be *palmate.* If there is only one midrib, from which smaller ribs extend both ways, the veining is said to be *pinnate* (meaning feather-like). Often the veining is intermediate between these two types.

FIG. 93. Netted veining (palmate) in leaf of melon

After Decaisne

107. Relation of shape to mode of veining. Since the water supply of the leaf is carried through the veins, and since they support the softer parts between them, one would expect to find that the form of the leaf would bear a close relation to its mode of veining. This is the case, and in general palmately veined leaves are roundish, while pinnately veined ones are longer than they are wide. These differences are particularly noticeable in leaves in which the leaf blade is not all of one piece, — *divided leaves* (Figs. 95, 96).

Usually veins, near their origin, follow a pretty straight course. This is desirable, in order to carry water as speedily as possible from the base of the leaf to its tip. The arrangement of the veins in the leaves of most land plants is admirably adapted to strengthen the leaf and protect it from being torn. In many cases the last-named result is secured by a sort of "binding" of looped veins running around the margin, as is fairly well shown in Fig. 94.

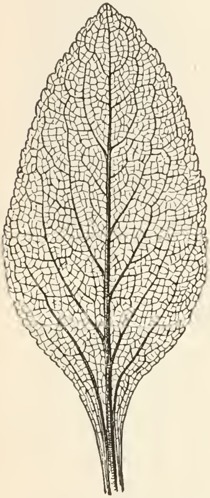

FIG. 94. Netted veining (pinnate) in leaf of foxglove

After Planchon

108. Description of leaf forms. The various forms of leaves are classed and described by botanists with great minuteness,[1] not simply for the study of leaves themselves, but also because in classifying and describing plants the characteristic shapes of the leaves of many kinds of plants form a simple and ready means of distinguishing them from each other and identifying them.

109. Occurrence of netted or parallel veining. With few exceptions, the leaves of monocotyledonous plants are parallel-veined and those of dicotyledonous plants netted-veined.

The needle-like leaves of the pines, spruces, firs, larches, and other coniferous trees have but a single vein, or two or three parallel ones; but in their case the veining could hardly be other than parallel, since the leaves are so narrow that no veins of any considerable length could exist except in a position lengthwise of the leaf.

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[1] See Kerner and Oliver, *Natural History of Plants*, Vol. I, pp. 623–637. See also Appendix to this book.

Monocotyledonous plants seldom have leaves with notched or cut margins, while dicotyledonous plants frequently have them.

A certain plan of venation is found mainly in plants with a particular mode of germination, of stem structure, and of arrangement of floral parts, and this is but one of the frequent cases in botany in which the structures of plants are correlated in a way which is not easy to explain.

No one knows why plants with two cotyledons should have netted-veined leaves, but many such facts as this are familiar to every botanist.

Fig. 95. Palmately divided leaf of buttercup

The blade of the leaf is discontinuous, consisting of several portions. — After Decaisne

110. Simple and compound leaves. The leaves so far studied are *simple leaves,* that is, leaves of which the blades are more or less entirely united into one piece. But while in the elm the margin is cut in only a little way, in some maples it is deeply cut in toward the bases of the veins. In some leaves the gaps between the adjacent portions extend all the way down to the petiole (in palmately veined leaves) or to the midrib (in pinnately veined ones). Such divided leaves are shown in Figs. 95 and 96.

Fig. 96. Pinnately divided leaf of celandine

After Decaisne

In still other leaves, known as *compound leaves,* or *branched leaves,* the petiole, as shown in Fig. 99 (*palmately compound*), or the midrib, as shown in Fig. 97 (*pinnately compound*), bears what look to be separate leaves. These differ in their nature and mode of origin from the portions of the blade of a divided leaf. One result of this difference appears in the fact that some time before the whole leaf is ready to fall in autumn, the leaflets of a compound leaf are seen to be jointed at their attachments. In Fig. 99 the horse-chestnut leaf is shown at the time of falling, with some of the leaflets already disjointed.

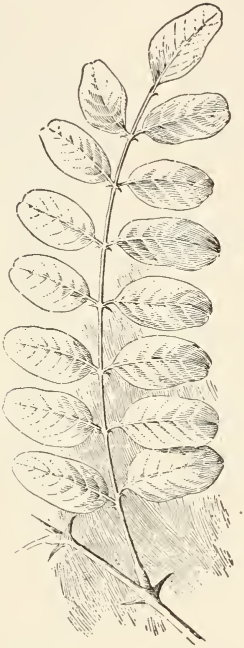

Fig. 97. Pinnately compound leaf of locust, with spines for stipules

Fig. 98. Pinnately compound leaf of pea

A tendril takes the place of a terminal leaflet.

That a compound leaf, in spite of the joints of the separate leaflets, is really only one leaf is shown: (1) by the absence of buds in the axils of leaflets (see Fig. 97); (2) by the horizontal arrangement of the blades of the leaflets, without any twist in their individual leafstalks; (3) by the fact that their arrangement on the midrib does not follow any of the systems of leaf arrangement on the stem (Sec. 111). If each leaflet of a compound leaf should itself become compound, the result would be to produce a *twice compound* leaf (Fig. 108).

FIG. 99. The fall of the horse-chestnut leaf

CHAPTER XI

LEAF ARRANGEMENT FOR EXPOSURE TO SUN AND AIR; HELIOTROPIC MOVEMENTS OF LEAVES AND SHOOTS

111. Leaf arrangement.[1] Leaves are quite generally arranged so as to secure the best possible exposure to the sun and air. This, in the vertical shoots of the elm, the oak (Fig. 100), the apple, beech, and other alternate-leaved trees, is quite consistent with their spiral arrangement. In horizontal twigs and branches of the elm, the beech (Fig. 101), the chestnut, the linden, and many other trees and shrubs, the desired effect is secured by the arrangement of all the leaves in two flat rows, one on each side of the twig. The rows are produced, as is easily seen on examining such a leafy twig, by a twisting about of the leafstalks. The adjustment in many opposite-leaved trees and shrubs consists in having each pair of leaves cover the spaces between the pair below it, and sometimes in the lengthening of the lower

Fig. 100. Leaf arrangement of the oak

Fig. 101. Leaf arrangement of European beech

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[1] See Kerner and Oliver, *Natural History of Plants*, Vol. I, pp. 396–424.

Plate II. Leaves arranged for maximum illumination

After F. E. Clements

leafstalks so as to bring the blades of the lower leaves outside those of the upper leaves. Examination of Figs. 102 and 103 will make the matter clear.

The student who observes the leafage of trees of different kinds on the growing tree itself may notice how circumstances modify the position of the leaves. Maple leaves, for example, on the ends of the branches are arranged much like those of the horse-chestnut, but they are found to be arranged more nearly flatwise along the inner portions of the branches, that is, the portions nearer the tree. Figs. 104 and 105 show the remarkable difference in arrangement in different branches of the Deutzia, and equally interesting modifications may be found in alternate-leaved trees, such as the elm and the cherry.

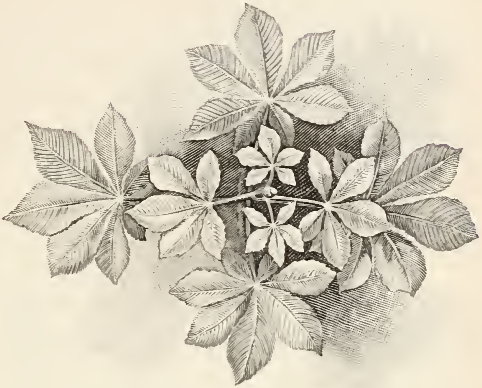

Fig. 102. Leaf arrangement of horse-chestnut on vertical shoots (top view)

After Kerner

Fig. 103. Leaf arrangement of horse-chestnut on vertical shoots (side view)

After Kerner

112. Leaf mosaics. In very many cases the leaves at the end of a shoot are so arranged as to form a rather symmetrical pattern, as in the horse-chestnut (Fig. 102).

When this is sufficiently regular, usually with the spaces between the leaves a good deal smaller than the areas of the leaves themselves, it is called a *leaf mosaic* (Fig. 106). Many of the most interesting leaf groups of this sort, as in the figure above mentioned, are found in the rosettes of the so-called root leaves of plants. Good examples of these are the dandelion, chicory, fall dandelion, thistle, hawkweed, *Pyrola*, and plantain. The leaves of these plants are kept from shading each other, sometimes by the narrowness of the leaves and sometimes by the lengthening of the leafstalks of the lower ones.

FIG. 104. Opposite leaves of *Deutzia*[1] (from the same shrub as Fig. 105) as arranged on a horizontal branch

113. Much-divided leaves. Not infrequently leaves are cut into slender, fringe-like divisions, as in the carrot, tansy, southernwood, wormwood, yarrow, dog fennel, cypress vine, and many other common plants. This kind of leaf seems to be adapted to offer considerable surface to the sun without cutting off too much light from other leaves underneath. Such a leaf is in much less danger of being torn by severe winds than are broader ones with undivided margins. The same purposes are served by

[1] *Deutzia crenata.*

compound leaves with very many small leaflets, such as those of the honey locust, the mimosa, acacia (Fig. 108), and other trees and shrubs of the pea family.

Fig. 105. Opposite leaves of *Deutzia*, as arranged on a vertical branch[1]

114. Daily movements of leaves. Many compound leaves have the power of changing the position of their leaflets to accommodate themselves to varying conditions of light and temperature. Some plants have the power of directing the leaves or leaflets edgewise towards the sun during the hottest parts of the day, allowing them to extend their surfaces more nearly in a horizontal direction during the cooler hours.

Fig. 106. Leaf mosaic of a *Campanula*

After Kerner

The so-called "sleep" of plants has long been known, but this subject has been most carefully studied rather recently. The wood sorrel, or oxalis, the common bean, clovers, and the locust tree are some of the most familiar of the plants whose leaves assume decidedly different positions at night from those which they occupy during the day. Sometimes the leaflets rise at night, and in many instances they drop, as in the red clover (Fig. 107) and the acacia (Fig. 108). One useful purpose, at any rate, that is served by the nocturnal position of the leaf is protection from frost. It has been proved experimentally that when

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[1] It will be noticed that the exposure to sunlight is here not nearly as favorable as in Fig. 104.

part of the leaves on a plant are prevented from assuming the folded position, while others are allowed to do so, and the plant is then exposed during a frosty night, the folded ones may escape, while the others are killed. Since many plants in tropical climates fold their leaves at night, it is certain that this movement has other purposes than protection from frost, and probably there is much yet to be learned about the meaning and importance of leaf movements.

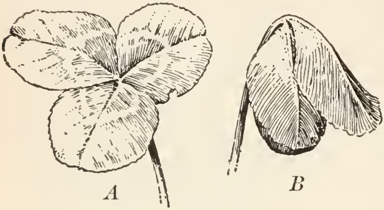

Fig. 107. A leaf of red clover

A, leaf by day; *B*, the same leaf at night

115. Self-induced movements; sensitive plants. Some leaves, notably those of the so-called telegraph plant,[1] have the power of maintaining pretty rapid movements without external stimuli. The small lateral leaflets of this plant, through a considerable range of temperatures above 72° F. (22° C.), in light or darkness alike, continue to move first up, then down, so that their tips make a complete circle in from one to three or more minutes. The motion is jerky, like that of the second hand of a watch, and gives one a vivid impression of the plant as a living thing.

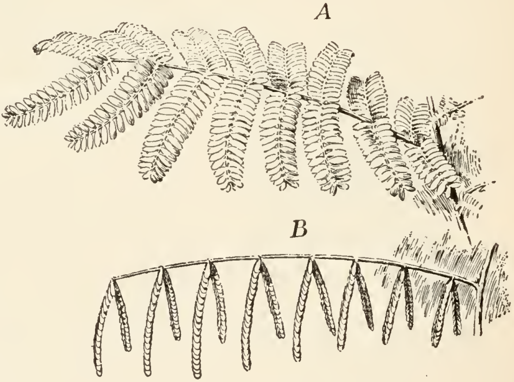

Fig. 108. A leaf of acacia

A, as seen by day; *B*, the same leaf at night. — After Darwin

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[1] *Desmodium gyrans.*

A good many plants of the pea family have leaflets which are sensitive to the touch. The best-known species is the common sensitive plant of the florists,[1] the leaflets of which close and drop, like those of Fig. 108, and the leafstalks droop when the plant is touched or jarred. Some of our common wild plants of the same family[2] have leaves which promptly show irritability when touched, and one species is locally known as "shame vine," from this peculiarity.

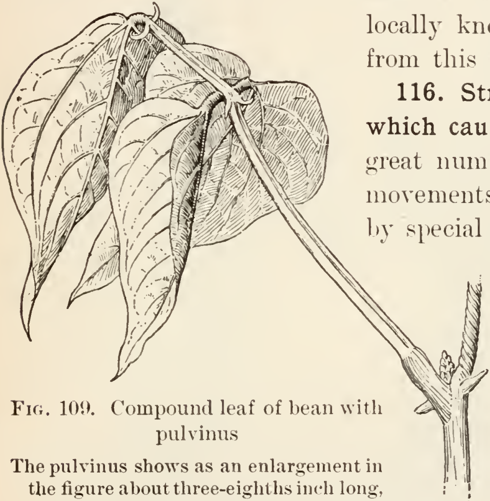

Fig. 109. Compound leaf of bean with pulvinus

The pulvinus shows as an enlargement in the figure about three-eighths inch long, at the base of the petiole. — After Sachs

116. Structure of the parts which cause leaf motions. In a great number of cases the daily movements of leaves are produced by special organs at the bases of the leafstalks. These cushion-like organs, called *pulvini* (Fig. 109), are composed mainly of parenchymatous tissue, which contains much water. It is impossible fully to explain in simple language the way in which the cells of the pulvini act, but in a general way it may be said that changes in the light to which the plant is exposed cause rather prompt changes in the amount of water in the cells in one portion or other of the pulvinus. If the cells on one side are filled fuller of water than usual, that side of the pulvinus will be expanded and make the leafstalk bend toward the opposite side. The promptness of these movements is no doubt in considerable measure due to the fact that in the pulvini, as in many other parts of plants, the protoplasm of adjacent cells is connected. Delicate threads of protoplasm extend through the cell walls, making the whole tissue a living

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[1] *Mimosa pudica.*

[2] Species of *Cassia* and *Desmanthus.*

web, so that any suitable stimulus or excitant which acts on one part of the organ will soon affect the whole organ.

117. Vertically placed leaves. Many leaves, like those of the olive (Fig. 111), always keep their principal surfaces nearly vertical. Thus they receive the morning and evening sun upon their faces, and the noonday sun (which is so intense as to injure them when received full on the surface) upon their edges.

Fig. 110. Leaves standing nearly vertical in compass plant (*Silphium laciniatum*)

A, view from east or west; *B*, from north or south. — After Kerner

This adjustment is most perfect in the compass plant of the prairies of the Mississippi basin. Its leaves stand nearly upright, many with their edges just about north and south (Fig. 110), so that the rays of the midsummer sun will, during every bright day, strike the leaf surfaces nearly at right angles during a considerable portion of the forenoon and afternoon, while at midday only the edge of each leaf is exposed to the sun.

FIG. 111. Nearly vertical leaves of the olive

118. Heliotropic movements. The whole plant above ground usually bends toward the quarter from which most light comes.

Any set of flowering plants growing close to a wall, or of house plants in a window, generally offers many illustrations of this principle. Movements caused by light are called *heliotropic movements* (from two words meaning turning toward light).

119. Positive and negative heliotropic movements; how produced. Plants may bend either toward or away from the strongest light. In the former case they are said to show *positive heliotropism,* in the latter *negative heliotropism.* In both cases the movement is produced by unequal growth, brought about by the stimulus of unequal lighting of different sides of the stem. A plant if placed on a revolving table before a window and slowly turned during the hours of daylight grows upright, like a plant out of doors. This is because it is not left with a one-sided illumination long enough to produce any bending.

CHAPTER XII

MINUTE STRUCTURE OF LEAVES; FUNCTIONS OF LEAVES*

120. Outline of leaf structure. Most foliage leaves of seed plants contain a rather complicated system of fibro-vascular bundles forming the *veins* (Sec. 105), which, taken together, constitute a framework by which the leaf is supported and strengthened. Over and around these veins lies a mass of green pulpy material, the spongy parenchyma. The whole leaf is covered by an epidermis. Frequently, especially in soft and rather thick leaves, such as those of the garden live-forever, the epidermis can be readily peeled off as a thin, transparent skin.

The epidermis and the spongy parenchyma decay far more readily than the woody framework, and so skeleton leaves may often be found on the ground in the spring, showing plainly the arrangement of the veins of the leaf.

121. Details of a leaf section. The relative positions and the detailed structure of the parts mentioned in Sec. 120 are best understood by reference to the magnified cross section of a typical foliage leaf.

In the ordinary leaf (Fig. 112) a section shows at the upper surface a layer of transparent cells of the epidermis *e*. Beneath this lies a layer of elongated cells *p*, of a green color, standing at right angles to the epidermis. These are called *palisade cells,* from a fancied resemblance of their shape and relative position to palisades. Under this layer the leaf interior is filled with an irregularly grouped mass of green cells known as the spongy parenchyma *sp*, throughout which occur numerous air spaces *a*,

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* To the Instructor: As the present chapter takes up its topics in considerable detail, it is suggested that it may be found expedient, if time is limited, to omit Secs. 129, 130, 132, 134, 139 (table), 145–147.

and in which is an occasional fibro-vascular bundle *b*. The palisade layer or layers and the spongy parenchyma are together known as *mesophyll* (meaning middle of leaf).

The lower surface of the leaf is covered by a layer of colorless epidermal cells *e′*, differing somewhat in size and shape from those of the upper epidermis.

The lower epidermis is pierced by many openings or stomata *s*. Each stoma opens into an air chamber. The upper epidermis of this leaf contains far less stomata than the lower one, and this is true of most leaves, — often the upper surface contains none.

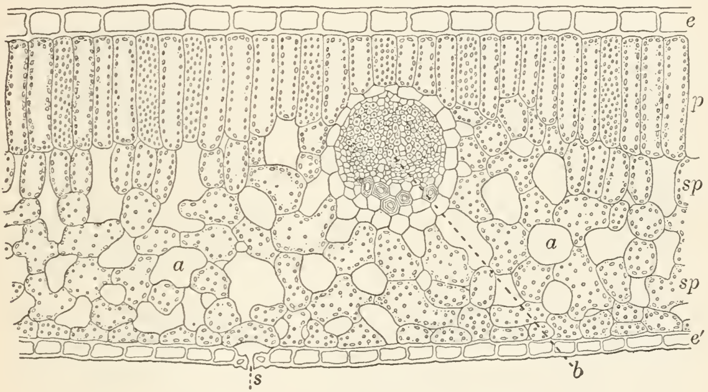

FIG. 112. Cross section of privet leaf

e, upper epidermis; *p*, palisade cells; *sp*, spongy parenchyma; *a*, air spaces; *b*, fibro-vascular bundle; *e′*, lower epidermis; *s*, stoma. Much magnified. — Modified after Giesenhagen

122. Uses of the parts above mentioned. It will be most convenient to discuss the uses of the parts of the leaf in detail a little later, but it will make matters simpler to state at once that the epidermis serves as a mechanical protection to the parts beneath and prevents excessive evaporation; that the palisade cells hold large quantities of the green coloring matter of the leaf in a position where it can receive enough but not too much sunlight; and that the cells of the spongy parenchyma share the work of the palisade cells, besides evaporating much water. The stomata admit air to the interior of the leaf, where the air spaces serve to store and to distribute it; they allow oxygen and carbon dioxide gas to escape; and, above all, they regulate the evaporation of water from the plant.

123. The epidermis. The cells of the epidermis are very generally filled with water. Their form and the thickness and material of their walls depend largely on the kind of soil and climate to which the plant is adapted. In most herbs the epidermal cells form only a single layer and are not greatly thickened.

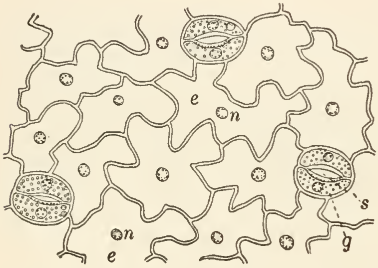

Fig. 113. Surface view of the epidermis of a buttercup leaf[1]

e, cells of epidermis; n, nuclei of epidermal cells; g, guard cell of stoma; s, stoma. Much magnified. — After Giesenhagen

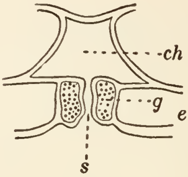

Fig. 114. Section through stoma of a buttercup leaf, at right angles to epidermis

e, epidermal cells; g, guard cell of stoma; s, stoma; ch, air chamber. Much magnified.—After Bonnier and Sablon

The stomata are not mere holes in the epidermis, but have a somewhat complicated structure. Each stoma consists of two kidney-shaped *guard cells* inclosing a slit-like opening into the leaf (Fig. 113).

When the stoma is viewed in a section at right angles to the surface of the leaf (Fig. 114) it appears as a narrow passage communicating with an air chamber inside the epidermis.

The number of stomata in a square inch of leaf surface is very great. An apple leaf contains about 24,000 and a black

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[1] Fig. 113 is from *Ranunculus Ficaria;* Figs. 114–118 from *R. acris.*

walnut leaf about 300,000 per square inch of the lower epidermis.

124. The mesophyll; chloroplasts; chlorophyll. The mesophyll appears to the naked eye of a uniform green, but under the microscope its cells are seen to contain many green structures called *chlorophyll bodies* or *chloroplasts* ("chlorophyll" meaning leaf green and "chloroplast" meaning molded out of green material). The color of the leaf, as well as that of green stems and other parts of the plant body, is due to these. A chloroplast is usually, in seed plants and in the higher spore plants, of an ellipsoidal form or lens-shaped and somewhat translucent. Its color is due to a green substance, soluble in alcohol but not in water, known as *chlorophyll.*

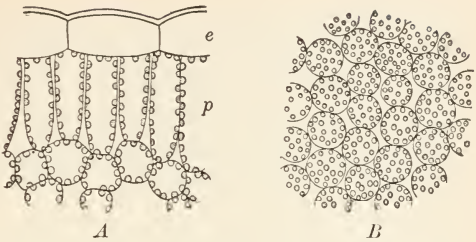

Fig. 115. Upper epidermis and palisade cells of a buttercup leaf

A, section perpendicular to upper surface; *B*, exterior view of upper surface with palisade cells seen through epidermis; *e*, epidermis; *p*, palisade cells. Much magnified. — After Bonnier and Sablon

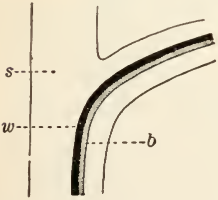

Fig. 116. Passage of a fibro-vascular bundle from stem to leaf of a buttercup (diagrammatic)

s, stem; *w*, woody part of bundle; *b*, sieve cells of bundle. — After Bonnier and Sablon

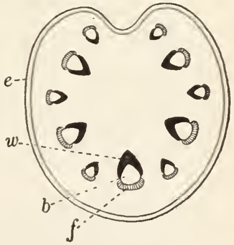

Fig. 117. Diagram of distribution of fibro-vascular bundles in the leafstalk of a buttercup

e, epidermis; *w*, woody part of bundle; *b*, sieve cells of bundle; *f*, fibrous layer on outer part of bundle. Magnified. — After Bonnier and Sablon

125. Woody tissue in leaves. The veins of leaves consist of fibro-vascular bundles containing wood fibers and vessels much like those of the stem of the plant. Indeed, these bundles in the leaf are continuous with those of the stem and consist merely of portions of the latter which pass outward and upward from the stem into the leaf under the name of *leaf traces.*

The manner in which fibro-vascular bundles pass from the stem through the petiole into the leaf and are there distributed can readily be gathered from an examination of Figs. 116–118. Their wood cells and vessels serve to carry water into the leaf, while their sieve cells carry plant food from its place of manufacture in the blade of the leaf down into the stem.

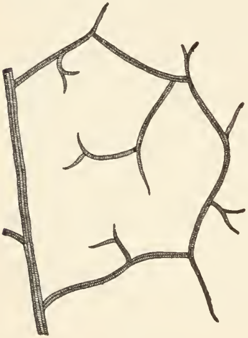

Fig. 118. Part of the fibro-vascular skeleton of a buttercup leaf

Much magnified. — After Bonnier and Sablon

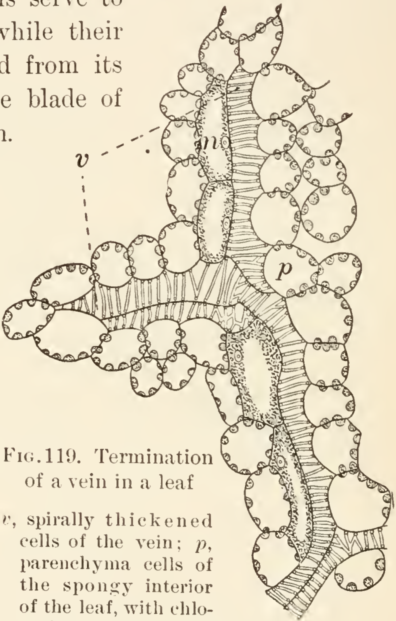

Fig. 119. Termination of a vein in a leaf

v, spirally thickened cells of the vein; *p*, parenchyma cells of the spongy interior of the leaf, with chlorophyll bodies; *n*, nucleated cells. × about 345 diameters

126. Nutrition. The series of processes by which the plant (1) takes up the raw materials to form its food, (2) unites these into foods, and finally (3) constructs tissue from these foods, or (4) stores them, constitutes *nutrition.*

A good deal of that portion of nutrition included under (1) is carried on by the roots. But all kinds of nutritive work are carried on in green leaves, and the portion numbered (2) is a specialty of green plant cells, particularly of those in leaves.

127. The work of leaves. A leaf has four principal functions:

1. Photosynthesis.
2. Respiration.
3. Assimilation.
4. Transpiration.

128. Photosynthesis. *All green leaves, when in healthy condition, at suitable temperatures and with sufficient illumination can produce carbohydrates (starch or sugars) from carbon dioxide and water.*

This process is of the greatest importance, since directly or indirectly all plants and animals depend upon it for their food supply. The manufacture by the plant of carbohydrates from the raw materials is known as *photosynthesis* (from two words meaning light and putting together). It is often called *fixation of carbon* or *assimilation of carbon.* Photosynthesis is performed by the chloroplasts, especially in the palisade cells, and goes on imperfectly or not at all in plants or parts of plants, as in certain parasites and other forms, in which no chlorophyll exists (Chapters XXII, XXX).

129. Chemical formula for photosynthesis. The details of the photosynthetic process are not wholly known, and it is not at all likely that in starch-producing plants starch is the first substance formed from carbon dioxide and water, but it is one of the early products of the action of the chloroplasts and is the easiest to detect by chemical tests applied to the leaf. In some plants, as the onion, the products of photosynthesis are all stored in the form of sugar.

If the chloroplast produced starch as the direct result of combining carbon dioxide and water, the chemical equation for the process would in its simplest form be[1]:

$$\left.\begin{array}{c}\text{Six molecules}\\ \text{of carbon}\\ \text{dioxide}\end{array}\right\} + \left\{\begin{array}{c}\text{Five mole-}\\ \text{cules of}\\ \text{water}\end{array}\right\} = \left\{\begin{array}{c}\text{One mole-}\\ \text{cule of}\\ \text{starch}\end{array}\right\} + \left\{\begin{array}{c}\text{Six molecules}\\ \text{of oxygen}\end{array}\right.$$

$$6\,CO_2 \quad + \quad 5\,H_2O \quad = \quad C_6H_{10}O_5 \quad + \quad 6\,O_2$$

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[1] Really some multiple of $C_6H_{10}O_5$ probably more nearly expresses the composition of starch than the simple formula given. It is certain that the photosynthetic process is much more complicated than a mere combination of carbon dioxide with water to form either starch or sugar.

If glucose (grape sugar) were the first product, the simplest equation would be:

$$6\,CO_2 + 6\,H_2O = C_6H_{12}O_6 \text{ (one molecule of glucose) } + 6\,O_2.$$[1]

It should be noticed that each of the processes above formulated results in the disappearance of six molecules of carbon dioxide and the production of six molecules of oxygen as a *waste product.*

These facts, namely, that in the green parts of plants exposed to sunshine carbon dioxide is consumed and oxygen liberated, form the foundation of our knowledge of photosynthesis. The first step in the study of the subject was taken by Joseph Priestley in 1771, by his discovering that air in which candles had been burned until they went out could be restored to something like its original condition by leaving in it for some time vigorous leafy sprigs of mint.

130. External conditions for photosynthesis. Photosynthesis can only occur:

1. When the plant is supplied with air containing carbon dioxide.
2. When the temperature is neither too high nor too low.
3. When the illumination is sufficient.

Ordinary air contains about one twenty-fifth of one per cent of its bulk of carbon dioxide. An increase of this amount up to four per cent, or one hundred times the normal quantity, increases photosynthesis, but a larger proportion usually at length proves injurious to the health of the plant.

Some arctic and alpine plants can perform the work of making carbohydrates at temperatures as low as the freezing point of water, but plants of warmer climates require a higher temperature. The rate of photosynthesis usually increases with rise of temperature up to about 77° F. (25° C.), after which it decreases.

Photosynthesis may go on very feebly, even in comparative darkness, but the light of the interior of ordinary rooms is

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[1] See Peirce, *Plant Physiology*, pp. 58–66.

insufficient for the vigorous growth of most seed plants excepting those which, in a wild condition, flourish in the shade. The rate of photosynthesis for most of the higher plants increases with the illumination up to a light intensity equal to that of full sunlight.

131. Conditions for formation of chlorophyll; its mode of action. Chlorophyll is usually produced only in plants grown in the light. Seedlings which have been sprouted in total darkness almost always have a white or very pale yellow color, and blanched celery affords a familiar example of the appearance of leaves grown in comparative darkness. Microscopical examination of thoroughly blanched plants shows them to be destitute of any decidedly green chloroplasts, and alcohol fails to extract from them the green chlorophyll solution which is readily obtained from ordinary leaves.

Iron must be present in the soil in order to enable the plant to form chlorophyll, and plants developed in water cultures absolutely free from iron remain yellow and grow feebly.

Chlorophyll appears to act by intercepting a considerable portion of the light rays which strike the leaf, thus compelling them to expend their energy on the chloroplasts and so to produce photosynthesis. If light traverses a substance with great ease, as it does pure dry air, for example, comparatively little effect is produced. On the other hand, when it strikes a substance which readily absorbs it, heating or chemical effects or both are produced, as is evident when a rough sheet of iron, a sensitized photographic dry plate, or blue-print paper is exposed to sunlight. Chlorophyll cannot itself do the work of photosynthesis, but it causes the light rays to act on the chloroplasts so that their protoplasm carries on the manufacture of carbohydrates from the raw materials.

132. Rate of starch making. The amount of starch manufactured daily by a given area of foliage must depend on the kind of leaves, the temperature of the air, the intensity of the sunlight, and some other conditions. Sunflower leaves and pumpkin or squash leaves produce starch at about the same rate. In a summer day fifteen hours long they can make nearly three quarters of an ounce for each square yard of leaf surface. A full-grown squash leaf has an area of about one and one-eighth square feet, and a plant may bear as many as a hundred of them. The entire plant would then produce nearly nine and a half ounces of starch per day.

Another way to emphasize the amount of work done by the leaves is to consider how much air would be needed to supply the carbon in a given weight of wood; for all this carbon has probably been derived from carbohydrates made in the leaves (or other green parts) by photosynthesis. If the wood of a tree after drying weighs 11,000 pounds and is half carbon, the latter would weigh 5500 pounds. Taking the carbon dioxide contents of the air at $\frac{4}{10,000}$, there would be more than 20,000,000 cubic yards of air needed to furnish the carbon of such a tree.[1]

The enormous amounts of carbon dioxide annually removed from the air by the growth of plants are continually being replaced by the respiration of animals, the decay of animal and vegetable material, and by the burning of fuel. From the burning of coal alone it is estimated that nearly 3,000,000 million pounds of carbon dioxide are every year returned to the atmosphere.

133. Respiration. Plants cannot carry on their life processes without consuming oxygen and giving off carbon dioxide and water. This oxygen consumption is the *respiration* of plants. Like animals, plants are dependent on the union of oxygen with oxidizable substances in their tissues for the energy with which they do the work of assimilation, growth, and reproduction,— in other words perform their life processes.

How oxygen can be made to combine with the carbon- and hydrogen-containing compounds in the plant at moderate temperatures is a problem which plant physiologists have not yet fully solved; but the union does constantly go on, and as a

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[1] Taken with slight alterations from Peirce, *Plant Physiology*, p. 44.

Plate III. A cypress swamp, the trees draped with Spanish moss (*Tillandsia*)

Modified, after H. J. Webber

result of the combination, water and carbon dioxide are continually excreted.

The amount of oxygen absorbed and of carbon dioxide given off is, however, so trifling compared with the amount of each gas passing in the opposite direction, while starch making is going on in sunlight at temperatures most favorable for photosynthesis, that under such circumstances it is difficult to observe the occurrence of respiration.

When the illumination is very feeble, from $\frac{1}{10}$ to $\frac{1}{40}$ that of bright, diffuse daylight, the manufacture of carbon dioxide by respiration and its consumption by photosynthesis are equal.

At high temperatures, such as 104° F. (40° C.), respiration may produce carbon dioxide more rapidly than photosynthesis can consume it, even with brilliant illumination.

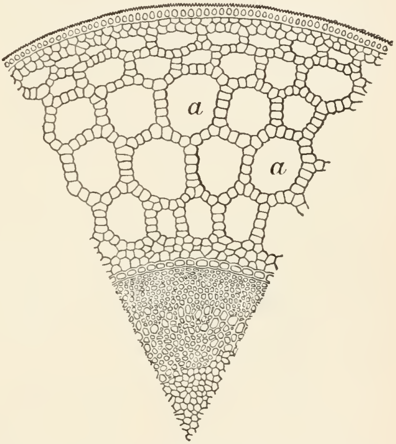

FIG. 120. Cross section of stem of marestail (*Hippuris*), with air passages *a*

After Baillon

In ordinary leafy plants the leaves, through their stomata, are the principal organs for absorption of air, but much air passes into the plant through the lenticels of the bark.

In partly submerged aquatics especial provisions are found for carrying the air absorbed by the leaves down to the submerged parts. This is accomplished in pond lilies by ventilating tubes which traverse the leafstalks lengthwise. In many cases such channels run up and down the stem (Fig. 120). In the American cypress (*Taxodium*) the "knees," which rise from the roots, as shown in Plate III, are thought to be for use in respiration, obtaining oxygen from the air and carrying it into the roots beneath the water.

134. Resting condition and diminished respiration. The whole plant body or parts of it may pass into a *resting condition,* in which growth is suspended and few manifestations of life are discernible. Familiar examples of this inactive condition are leafless trees in winter, and rootstocks, tubers, and bulbs during the winter of ordinary temperate climates or the rainless summer of southern California and the Mediterranean coast region. Seeds and many kinds of resting spores afford extreme instances of the possibility of a suspension of activity for years, followed by prompt growth when suitable conditions are supplied. In general, a moderately low temperature and dryness favor the resting state. During the resting period respiration is greatly diminished, so much so in the case of thoroughly dry seeds as to be almost or quite imperceptible.

When resting protoplasm is placed in circumstances which enable it to begin active respiration, growth and development soon appear. Thus twigs of lilac or other shrubs will flower after a time, when placed in water and brought into a warm room in winter.

In many cases, as with most seeds, the period of repose is essential for growth. Potato tubers will not sprout as soon as they are mature: some varieties need only two months and others four or five months of rest.

135. Assimilation. By most American plant physiologists[1] the word *assimilation* is used as a name for the series of changes by which the plant transforms absorbed or manufactured food into the materials of its own tissues.

The transformation of starch or sugar into substances, like cellulose, which consist of the same elements (carbon, hydrogen, and oxygen) differently combined, is a relatively simple matter; but the manufacture from carbohydrates of such very complex nitrogenous substances as the proteids and living protoplasm is a most complicated process, and imperfectly understood.

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[1] European botanists often include in the term assimilation both photosynthesis and the processes discussed in this section.

136. Contrast between photosynthesis and respiration

	OCCURRENCE	RELATION TO LIGHT	RELATION TO TEMPERATURE	CONSUMES	PRODUCES	EFFECT UPON STORES OF ENERGY-PRODUCING MATERIAL IN PLANT
Photosynthesis	In cells with chlorophyll	Requires light	Increases from 32° to 77° F. (0° to 20° C.), then decreases	Carbon dioxide	Starch and sugars; oxygen as waste product	Increases
Respiration	In all living cells	Independent of light	Increases with rise of temperature till plant is permanently injured by heat. No definite maximum	Oxygen	Carbon dioxide as waste product	Decreases

Probably diastase or some other ferment in the green parts of the plant transforms the newly made starch into sugar, and some of this is apparently combined on the spot with nitrogen, sulphur, and phosphorus. These elements are derived from nitrates, sulphates, and phosphates, taken up in a dissolved condition by the roots of the plant and transported to the leaves. The details of the process are not understood, but the result of the combination of the sugars or similar substances with suitable (very minute) proportions of nitrogen, sulphur, and phosphorus is to form complex nitrogen compounds. These are not precisely of the same composition as the living protoplasm of plant cells or as the reserve proteids stored in seeds (Secs. 8, 12), stems (Sec. 66), and other parts of plants, but are readily changed into protoplasm or proteid foods as necessity may demand.

Assimilation is by no means confined to leaves; indeed, most of it, as above suggested, must take place in other parts of the plant. For instance, the manufacture of the immense amounts of cellulose, of cork, and of the compound (*lignin*) characteristic of wood fiber, which go to make up the main bulk of a large tree, must be carried on in the roots, trunk, and branches of the tree.

137. Metabolism. It is convenient to have a single word to express all the chemical changes which are controlled by the living protoplasts. Such a word is *metabolism.* It embraces all the nutritive processes mentioned in Sec. 126, as well as respiration and the chemical changes concerned in the excretion of waste materials.

There are two principal types of metabolic processes, — *constructive* metabolism (such as photosynthesis), which unites simpler compounds into more complex ones, and *destructive* metabolism (such as respiration), which breaks up complex substances into simpler ones.

Digestive metabolism, performed by means of various ferments, begins, as already mentioned, in the seed during germination and is carried on in most parts of the higher plants during all active periods of their lives. It is especially energetic in removing

138. Tabular summary of metabolic and other processes[1]

Name of Process	By what Apparatus or Agency carried on	By what Kind of Energy carried on	Substances acted on	Useful Products	Waste Products
Photosynthesis	Chlorophyll bodies of leaves and green stems	Sunlight and heat, energy of protoplasm	Carbon dioxide and water	Sugar and starch	Oxygen, passed out of stomata
Respiration	All live cells of interior of root, stem, or leaf, when supplied with air	Chemical attraction between oxygen and combustible substances	Sugars and oils	Energy (i.e. power to do work)	Carbon dioxide, and water
Digestion	Various ferments or enzymes		Starch, cellulose, stored proteids	Sugars, proteids in soluble forms	
Assimilation (tissue building)	Living protoplasm in leaves and any growing parts of the plant		Sugar and compounds containing nitrogen, sulphur, and phosphorus	Proteids for storage. Protoplasm for live, active cells	
Excretion of water (transpiration)	Cells of pulpy interior of leaf around air spaces; other cells beneath stomata in stems and elsewhere	Heat, vaporizing water	Soil water brought up from roots	Potassium salts and other useful inorganic compounds stored	Water vapor, passed out of stomata. Lime salts, silica, etc., deposited in the leaf or stem

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[1] It is to be understood that this table only includes a small portion of the whole series of metabolic processes which go on in green plants, but it embraces some of the most important ones. Excretion of water is not a metabolic process, but is inserted here for the purpose of making the showing of the work of the leaf as complete as possible.

the newly formed starch from the green cells of leaves for use in other parts of the plant body. Much of this food (carried about in the form of a solution of sugar) is used for building material, as suggested in Sec. 136; but a good deal of it is often transported to parenchyma cells of the stem and the roots, where it is changed back into starch for storage. This change is accomplished by small structures known as *leucoplasts* in the cells. Each leucoplast may cause a deposit, upon some part of its outer surface, of successive layers which finally develop into a complete starch grain. How the leucoplast is able to bring about the change from starch to sugar is unknown.

139. Transpiration. The process of giving off water in the form of vapor from the stomata of plants is called *transpiration.* It is not a mere drying up, such as occurs when a pile of seaweeds or a split stick of cord wood is exposed to dry air, but is an important function of the leaves of most seed plants and of the higher spore plants. In such forms as the cactuses (Fig. 50), which are practically leafless, transpiration is performed by the epidermis of the stem.

As already mentioned (Sec. 36), ordinary terrestrial seed plants are, during the active periods of their lives, continually absorbing water through the roots. This water brings with it dissolved salts from the soil, many of which are used in the tissue-forming work of the plant body. Some of the water, but only an insignificant portion of the whole amount, is needed for photosynthesis, and a good deal of it is useful in carrying the soluble plant foods, such as sugars, to the growing parts; but there remains a large excess of water to be excreted, and this duty is mainly performed by the mesophyll, and its amount is regulated by the epidermis of the leaves. The air within the intercellular spaces of the mesophyll is surrounded by thin-walled cells filled with watery protoplasm, and it must therefore be nearly or quite saturated with moisture. When allowed to escape from the leaf this air rapidly carries off quantities of watery vapor.

140. Uses of the epidermis.[1] The epidermis, by its toughness, tends to prevent mechanical injuries to the leaf. After the change of the outer portions of its cell walls into a corky substance it greatly diminishes evaporation from the general surface. This process of becoming filled with cork material, *suberin* (or a substance of similar properties known as *cutin*), is essential to the safety of leaves or of young stems which have to withstand heat and dryness. The corky or cutinized cell wall is waterproof, while ordinary cellulose allows water to soak through it with ease. Merely examining sections of the various kinds of epidermis will not give nearly as good an idea of their properties as can be obtained by studying during severe droughts the behavior of plants which have strongly cutinized surfaces and of those which have not, or by exposing thin-leaved plants and thick leathery-leaved ones to a very dry atmosphere without watering. Fig. 121, however, may convey some notion of the difference between the two kinds of structure.

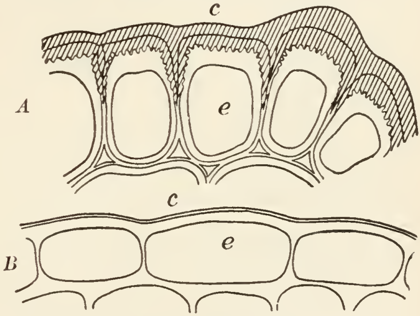

Fig. 121. Unequal development of cuticle by epidermis cells

A, epidermis of butcher's broom (*Ruscus*); *B*, epidermis of sunflower; *c*, cuticle; *e*, epidermis cells. — After Frank and Tschirch

In *A* the shaded part is all cutinized; it consists of the thick cuticle proper and, beneath this, cutinized layers of cell wall, under which is a heavy layer of cellulose. In *B* the cuticle is thin, and the outer portion of the cell walls consists wholly of cellulose.

In most cases, as in the india-rubber tree, the external epidermal cells (and often two or three layers of cells beneath these) are filled with water, and thus serve as reservoirs from

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[1] See Kerner and Oliver, *Natural History of Plants*, Vol. I, pp. 273–362.

which the outer parts of the leaf and the stem are at times supplied.

In many cases, noticeably in the cabbage, the epidermis is covered with a waxy coating, which doubtless increases the power of the leaf to retain needed moisture, and which certainly prevents rain or dew from covering the leaf surfaces, especially the lower surfaces, so as to hinder the operation of the stomata. Many common plants, like the meadow rue and the nasturtium, possess this power to shed water to such a degree that the under surface of the leaf is hardly wet at all when immersed in water. The air bubbles on such leaves give them a silvery appearance when held under water.

141. Operation of the stomata. The stomata serve to admit air to the interior of the leaf and to allow moisture in the form of vapor to pass out of it. They do this not in a passive way, as so many mere holes in the epidermis might, but to a considerable extent they regulate the rapidity of transpiration, opening more widely in damp weather and in sunlight, and closing in very dry weather. The opening is caused by each of the guard cells bending into a more kidney-like form than usual, and the closing by a diminution of *turgor* and straightening out of the guard cells.

The details of the mechanical explanation of stoma movements are complicated, and it is difficult fully to account for their irritability in response to light, heat, and moisture stimuli, and to variations in the amount of salts in the water absorbed by the roots.

142. Location of the stomata. The under side of the leaf, free from palisade cells, abounding in intercellular spaces, and pretty well protected from becoming covered with rain or dew, is especially adapted for the working of the stomata, and accordingly we usually find them in much greater numbers on the lower surface. On the other hand, stomata occur only on the upper surface of the leaves of pond lilies, which lie flat on the water. In those leaves which stand with their edges nearly vertical, the stomata are distributed somewhat equally on both surfaces. Stomata occur in the epidermis of young stems, being replaced later by the lenticels.

The health of the plant depends largely on the proper working condition of the stomata, and one reason why plants in cities often fail to thrive is that the stomata become choked with dust and soot. If the stomata were to become filled with water, their activity would cease until they were freed from it; hence many plants have their leaves, especially the under surface, protected by a coating of wax which sheds water.

143. Hairs on leaves. Many kinds of leaves are more or less hairy or downy, as those of the mullein, the "mullein pink," many cinquefoils, and other common plants. In some instances this hairiness may be a protection against snails or other small leaf-eating animals, but in other cases it seems to be pretty clear that the woolliness (so often confined to the under surface) is to lessen the loss of water through the stomata. The Labrador tea is an excellent example of a plant with a densely woolly coating on the lower surface of the leaf. The leaves, too, are partly rolled up like those of the crowberry (Fig. 361), but less completely, with the upper surface outward, so as to give the lower surface a sort of deeply grooved form, and on the lower surface all of the stomata are placed. This plant, like some others with the same characteristics, ranges far north into regions where the temperature, even during summer, often falls so low that absorption of water by the roots ceases, since it has been shown that this nearly stops a little above the freezing point of water. Exposed to cold, dry winds, the plant would then often be killed by complete drying if it were not for the protection afforded by the woolly, channeled under surfaces of the leaves.

144. Total amount of transpiration. In order to prevent wilting, the rise of sap during the life of the leaf must have kept pace with the evaporation from its surface. The total amount of water that travels through the roots, stems, and leaves of most seed plants during their lifetime is large, relative to the weight of the plant itself. During 173 days of growth a corn plant has been found to give off nearly 31 pounds of water. During 140 days of growth a sunflower plant gave off about 145 pounds. A grass plant has been found to give off its own weight of water every twenty-four hours in hot, dry summer weather. This would make about 6½ tons per acre every twenty-four hours for an ordinary grass field, or rather over 2200 pounds of water from a field 50 × 150 feet, — that is, from a tract not larger than a good-sized city lot. Calculations based on observations made by the Austrian forest experiment stations showed that a birch tree with 200,000 leaves, standing in open ground, transpired on hot summer days from 700 to 900 pounds, while at other times the amount of transpiration was probably not more than 18 to 20 pounds.[1]

145. Accumulation of mineral matter in the leaf. Just as a deposit of salt is found in the bottom of a seaside pool of salt water which has been dried up by the sun, so old leaves are found to be loaded with mineral matter left behind as the sap drawn up from the roots is evaporated through the stomata. A bonfire of leaves makes a surprisingly large heap of ashes. An abundant constituent of the ashes of burnt leaves is silica, a substance chemically the same as sand. This the plant is forced to absorb along with the potash, compounds of phosphorus, and other useful substances contained in the soil water; but since the silica is of hardly any value to most plants, it often accumulates in the leaf as so much refuse. Lime is much more useful to the plant than silica, but a far larger quantity of it is absorbed than is needed; hence it, too, accumulates in the leaf.

146. The fall of the leaf. In the tropics trees retain most of their leaves the year round; a leaf occasionally falls, but no considerable portion of them drops at any one season.[2] The same

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[1] See B. E. Fernow's discussion in Report of Division of Forestry of United States Department of Agriculture, 1889; also the article, "Water as a Factor in the Growth of Plants," by B. T. Galloway and Albert F. Woods, *Year-Book of United States Department of Agriculture*, 1894.

[2] Except where there is a severe dry season.

statement holds true in regard to our cone-bearing evergreen trees, such as pines, spruces, and the like. But the impossibility of absorbing soil water when the ground is at or near the freezing temperature would cause the death, by drying up, of trees with broad leaf surfaces in a northern winter. And in countries where there is much snowfall, most broad-leafed trees could only escape injury to their branches from overloading with snow, by encountering winter storms in as close-reefed a condition as possible. For such reasons our common shrubs and forest trees (except the cone-bearing, narrow-leafed ones already mentioned) are mostly *deciduous,* — that is, they shed their leaves at the approach of winter. There are, however, in the eastern United States a few species of broad-leafed evergreen trees and large shrubs, such as the live oak, some *Rhododendrons,* the mountain laurel (*Kalmia*), and the hollies. Along the Pacific coast there are many more forms, including five fairly common species of evergreen oaks, the beautiful *Arbutus,* and the manzanitas (*Arctostaphylos*).

Looking somewhat closely into the matter of deciduousness of the trees and shrubs of temperate climates (not including the coniferous species), one finds that they may be classed as follows:

I. Leaves simultaneously deciduous	A, winter deciduous B, summer deciduous
II. Leaves not simultaneously deciduous (evergreen)	C, leaves some of them lasting two years or more D, leaves lasting more than one year but less than two

The only one of the four subdivisions which shows fairly constant leafage at all seasons is the one designated as *C.* Leaves of the subdivision *D* often fall when about fifteen months old, so that the tree is unusually leafy during the three months when the new leaves are developing to their full size, but before the old ones begin to fall. It is a noteworthy fact that in many species of broad-leafed evergreens, for example the ilex oak, the oleander, and *Smilax aspera*, the leaves do not attain their maximum power of transpiration as soon as they are fully grown. Such a leaf transpires more when fifteen months old than when three months old.

The fall of the leaf is preceded by important changes in the contents of its cells. Much of the sugary and protoplasmic contents of the leaf disappears before it falls. These valuable materials have been absorbed by the branches and roots, to be used again the following spring.

The separation of the leaf from the twig is accomplished by the formation of a layer of cork cells across the base of the petiole in such a way that the latter finally breaks off across the surface of the layer. A waterproof scar is thus already formed before the removal of the leaf, and there is no waste of sap dripping from the wound where the leafstalk has been removed, and no chance for fungi to attack the bark or wood and cause it to decay. In compound leaves each leaflet may become separated from the petiole, as is notably the case with the horse-chestnut leaf (Fig. 99). In woody monocotyledons, such as palms, the leafstalks do not commonly break squarely off at the base, but wither and leave projecting stumps on the stem.

The brilliant coloration, yellow, scarlet, deep red, and purple, of autumn leaves is popularly but wrongly supposed to be due to the action of frost. It depends merely on the changes in the chlorophyll grains and the liquid cell contents that accompany the withdrawal of the proteid material from the tissues of the leaf. The chlorophyll turns into a yellow, insoluble substance after the valuable materials which accompany it have been taken away, and the cell sap at the same time may turn red. Frost perhaps hastens the break-up of the chlorophyll, but individual trees often show bright colors long before the first frost, and in very warm autumns most of the changes in the foliage may come about before there has been any frost.

CHAPTER XIII

THE FLOWER OF THE HIGHER SEED PLANTS

147. Organs of the flower. The parts found in a complete flower of the higher seed plants (angiosperms) are *sepals, petals, stamens,* and *pistils* (Fig. 122). The sepals, taken together, constitute the *calyx;* the petals, taken together, constitute the *corolla.* The calyx and corolla are collectively known as the *floral envelopes,* or *perianth.*

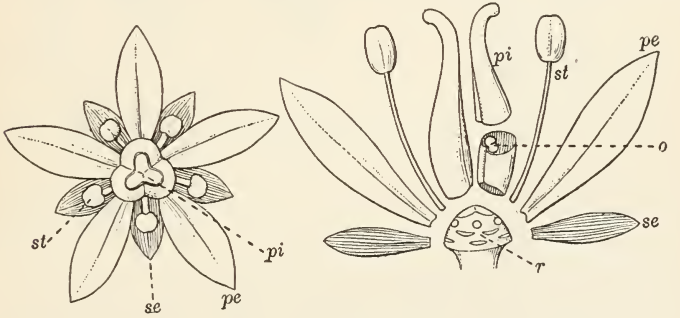

Fig. 122. Face view and dissection of an angiospermous flower

r, receptacle; *se*, sepal; *pe*, petal; *st*, stamen; *pi*, pistil; *o*, ovule

Many angiospermous flowers consist of five circles, or whorls, two of which belong to the perianth, two to the stamens, and one to the pistils. The parts of each circle alternate in position with those of the preceding or following one, and all the members of each circle are alike (Fig. 122).

148. Suppression and multiplication of circle. Any circle, or part of a circle, may be suppressed. If one set of parts of the perianth is lacking it is assumed to be the corolla (Fig. 123).[1]

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[1] For other instances of suppression of various sets, see Bergen, *Flora of the Northern States* (Figs. 3, 8, 9, 11, 16).

A whorl of stamens is frequently suppressed, so that only one circle is present in the flower (Fig. 128).

Multiplication of whorls is particularly frequent among the stamens, but other whorls may also show it (see Figs. 149, 150).

Fig. 123. Flower of (European) wild ginger, with calyx but no petals

After Wossidlo

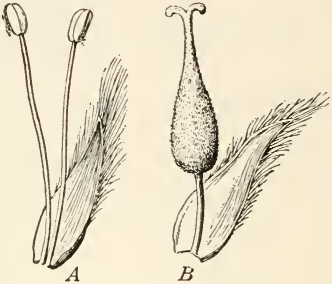

Fig. 124. Flowers of willow

A, staminate flower; *B*, pistillate flower. Magnified. — After Decaisne

149. Unisexual flowers. The stamens and pistils may be produced in separate flowers, which are *unisexual* (often called *imperfect*) flowers. In the very simple unisexual flowers of the willow (Fig. 124) each flower of the catkin (Fig. 143) consists merely of a pistil or a group of (usually two) stamens springing from the axil of a small bract.

Fig. 125. Bilaterally symmetrical flower of pansy

Staminate and pistillate flowers may be borne on different plants, as they are in the willow, or they may be borne on the same plant, as in the hickory and the hazel among trees, or in the castor-oil plant, Indian corn, and the begonias. When staminate and pistillate flowers are borne on separate plants, such a plant is said to be *diœcious*, that is of two households; when both kinds of flower appear on the same individual, the plant is said to be *monœcious*, that is of one household.

150. Symmetry of the flower. Most angiosperms have symmetrical flowers. The simplest are those whose parts are arranged as in Figs. 122, 128, and 149, having *radial symmetry.*[1]

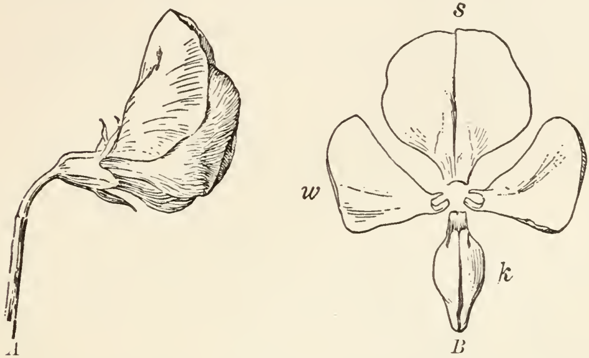

Fig. 126. Bilaterally symmetrical flower of sweet pea

A, side view; *B*, front view, dissected; *s*, standard; *w*, *w*, wings; *k*, keel

A higher type of flower is that which shows *bilateral symmetry,*[2] as in Figs. 125 and 126.

If the drawing of such a flower were folded along the axis of symmetry, one half of the drawing would cover and correspond with the other half. Some flowers are wholly irregular, showing no sort of symmetry.

151. The receptacle. The parts of the flower are borne on a variously formed expansion of the flower stalk known as the *receptacle.* Usually, as in Fig. 122, this is only a slight enlargement of the flower stalk, but in the rose (Fig. 127), the pond lily (Fig. 137), the magnolia, the *Calycanthus*, and a good many other familiar flowers it is large and conspicuous.

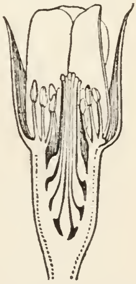

Fig. 127. A rose
Longitudinal section
After Decaisne

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[1] Such flowers are also called *actinomorphic*, meaning ray-formed.

[2] These are called *zygomorphic* flowers (from Greek words signifying *yoke* and *form*). In many floras these are described as irregular flowers.

152. The perianth. In dicotyledonous plants the sepals, or divisions of the calyx, are commonly green and somewhat leaf-like. The petals in showy flowers are of many colors, ranging all the way from violet to red. Either whorl of the perianth may be found to have assumed some very peculiar form, to carry out the purpose of the flower, as is briefly explained in Chapter XXXII.

Among the lower families of angiosperms the parts of the perianth are frequently all *distinct*, as shown in Figs. 122 and 134. Among the higher families the members of the perianth are often borne upon a tubular or cup-like outgrowth from the receptacle (Fig. 136, *B*), so that the sepals or petals, or both, appear to have grown together more or less completely.[1]

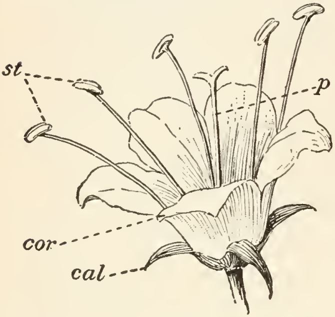

Fig. 128. Flower of *Hydrophyllum*
cal, lobe of calyx; *cor*, lobe of corolla; *st*, stamens; *p*, pistil. Modified. — After Lindley

When the calyx or the corolla is borne upon a tubular, bowl-shaped, or other extension of the receptacle, there are often divisions, teeth, or lobes at the rim of the tube (Figs. 128, 144, Appendix) showing how many sepals or petals the flower possesses. Special names are given to a large number of forms of the sympetalous corolla, and these are of much use in accurate descriptions of seed plants. A few of these are illustrated in Chapter XXXII and in the Appendix.

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[1] When the parts of the perianth are distinct the calyx is said to be *chorisepalous* and the corolla *choripetalous;* other terms are *polysepalous* and *polypetalous.* When the receptacle forms a cup-like or tubular outgrowth so that the teeth or lobes of this alone are sepals or petals, the flower is said to be *synsepalous* or *sympetalous ;* other terms are *gamosepalous* or *gamopetalous. Choris* means apart, *poly* means many, *syn* means together, *gamos* means marriage. Botanists have until recently used such expressions as "sepals united into a tube," etc., but these are incorrect.

153. Form of the stamen; union of stamens. Stamens are of many specialized forms, to adapt them to their functions in flowers of various shapes, but many are of the shape shown in Fig. 129. Such a stamen consists of an expanded part, the *anther*, borne on a stalk called the *filament*. Anthers are often nearly or quite *sessile* (seated, i.e. destitute of filaments). Inside the anther is the powdery or pasty substance called *pollen* (Fig. 153).

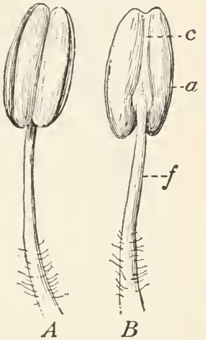

Fig. 129. Parts of a stamen

A, front; *B*, back; *a*, anther; *c*, connective; *f*, filament. — After Strasburger

Stamens may be wholly unconnected with each other, or *distinct*, as shown in Figs. 122, 124, and 128, or they may be really or apparently more or less united to each other. In Fig. 130 the stamens have arisen separately, but finally become joined together by their anthers (as is always the case in the family *Compositæ*). In other cases the stamens appear united when they are not really so, because they are borne on a ring or tube of tissue, as already explained in connection with the perianth (Sec. 152).

Fig. 130. Stamens of a thistle, with anthers united into a ring

a, united anthers; *f*, filaments, bearded on the sides. — After Baillon

Without regard to whether the union is real or apparent, stamens which occur in a single group (the filaments appearing joined) are said to be *monadelphous* (Fig. 131), in two groups, *diadelphous* (Fig. 132), in many groups, *polyadelphous* (the terms meaning one brotherhood, two brotherhoods, many brotherhoods).

154. The carpel. The simplest form of the organ which bears the structures called *ovules*, that are to mature into seeds, is known as the *carpel*.

In the lowest of the two great groups of seed plants, the *gymnosperms* (meaning naked seeds), to which the pines, spruces, cedars, and the like belong, the ovules are borne exposed on the surface of the carpels, which usually have the form of scales. But in the higher group of seed plants, the *angiosperms* (meaning seeds in a vessel), the carpels constitute a part of cases or chambers in which the ovules are formed and which are generally quite closed.

Fig. 131. Monadelphous stamens of mallow

155. The pistil. The term *pistil* (Latin for pestle) is applied to the closed structure which contains the ovules and is formed by the carpels of the angiosperms. This is a more general term than carpel, for it applies to organs composed of one or of several carpels. If a pistil is of one carpel it is said to be *simple,* if of two or more carpels it is *compound.*

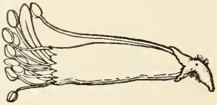

Fig. 132. Diadelphous stamens of sweet pea

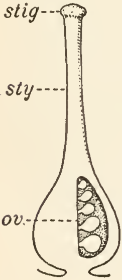

Fig. 133. Parts of the pistil

ov, ovary; *sty*, style; *stig*, stigma

The pistil often consists of an enlarged, hollow portion containing ovules and known as the *ovary,*[1] a stalk-like *style,* and a knob or ridged expansion called the *stigma* (Fig. 133). Not infrequently the style is wanting and the stigma is *sessile* (seated) on the ovary.

A flower may contain several or many carpels in the form of simple pistils separate from one another, as in the stonecrop and the buttercup (Figs. 134, 161). When several carpels form a compound pistil the manner and extent of the union is various.

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[1] The term *ovary* is an unfortunate one, since it would seem to mean the organ which bears eggs. Those who wish to avoid the use of the term may substitute the word *ovulary*, proposed by Professor Charles R. Barnes, or may simply say *ovule case*.

The union generally forms the ovary, although this is sometimes developed in large part as a cup-like or tubular growth from the stem under the carpels. Sometimes the union is so complete that the compound pistil has only one style and one stigma; but frequently the styles remain separate, or the styles may be united and the stigmas separate, or at least lobed so as to show of how many carpels the pistil is made up (Figs. 123, 124). Even when there is no external sign to indicate the compound nature of the pistil, it can usually be recognized from a study of a cross section of the ovary.

Fig. 134. Flower of stonecrop

A, entire flower; *B*, vertical section. — After Decaisne

156. Locules of the ovary; placentas. Compound ovaries very commonly consist of a number of separate chambers known as *locules*.[1] Fig. 135, *B*, shows a three-loculed ovary seen in cross section. The ovules are not borne indiscriminately by any part of the lining of the ovary. In one-loculed pistils they frequently grow in a line running along one side of the ovary, as in the pea pod (Fig. 343). The ovule-bearing line is called a *placenta;* in compound pistils there are commonly as many placentas as there are separate carpels joined to make the

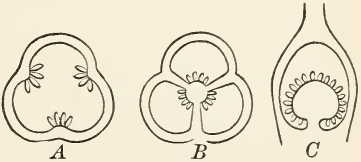

Fig. 135. Principal types of placenta

A, parietal placenta; *B*, central placenta; *C*, free central placenta; *A* and *B*, transverse sections; *C*, longitudinal section. — After Strasburger

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[1] Often (less correctly) called *cells*.

pistil. Placentas on the wall of the ovary, like those in Fig. 135, *A*, are called *parietal placentas;* those which occur as at *B* are said to be *axial;* and those which, like the form represented in *C*, consist of a column rising from the bottom of the ovary are called *free central placentas.*

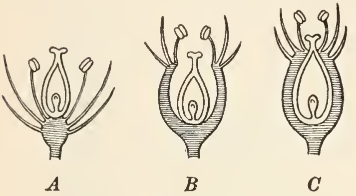

Fig. 136. Insertion of the floral organs

A, hypogynous, all the other parts on the receptacle, beneath the pistil; *B*, perigynous, petals and stamens apparently growing out of the calyx, around the pistil; *C*, epigynous, all the other parts appearing to grow out of the pistil. — After Strasburger

157. Superior, half-inferior, and inferior ovaries. When, as in the diagrammatic flower of Fig. 122, the receptacle is rounded or club-shaped, and the floral organs arise from it in successive sets, the flower is said to be *hypogynous* (from two Greek words here applied to mean under the pistil), and the ovaries are said to be *superior* (Fig. 136, *A*).

When the receptacle is concave, or when it grows up about the pistil, carrying the other floral parts with it, so that the pistil is inserted on the same level with the stamens or lower, but not at all united with the receptacle, the flower is said to be *perigynous* (meaning around the pistil) and the ovary is *half inferior* (Fig. 136, *B*).

When the ovary is united with the receptacle the flower is said to be *epigynous* (meaning upon the pistil), or the ovary is *inferior* (Fig. 136, *C*).

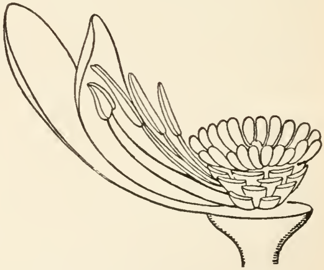

Fig. 137. White water lily

The inner petals and the stamens growing from the ovary. — After Decaisne

158. Floral diagrams. Sections (real or imaginary) through the flower lengthwise, like those of Fig. 136, help greatly in giving an accurate idea of the relative position of the floral organs. Equally important in this way are cross sections, which may be recorded in diagrams like those of Fig. 138.[1] In constructing such diagrams it will often be necessary to suppose some of the parts of the flower to be raised or lowered from their true position, so as to bring them into such relations that all could be cut by a single section. This would, for instance, be necessary in making a diagram for the cross section of the flower of the white water lily, of which a partial view of one side is shown in Fig. 137.

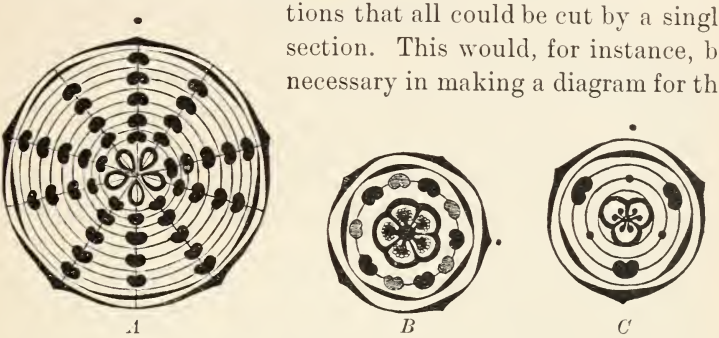

Fig. 138. Diagram of cross sections of flowers

A, columbine; *B*, heath family; *C*, *Iris* family. In each diagram the dot alongside the main portion indicates a cross section of the stem of the plant. In *B* every other stamen is more lightly shaded, because some plants of the heath family have five and some ten stamens. — After Sachs

It is found convenient, in diagrams of cross sections, to distinguish the sepals from the petals by representing the former with midribs. The diagrammatic symbol for a stamen stands for a cross section of the anther, and that for the pistil is a section of the ovary. If any part is lacking in the flower (as in the case of flowers which have some antherless filaments), the missing or abortive organ may be indicated by a dot. In the diagram of the *Iris* family (Fig. 138, *C*) the three dots inside the flower indicate the position of a second circle of stamens, found in most flowers of monocotyledons but *not* in this family.

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[1] For floral diagrams see Le Maout and Decaisne, *Traité Général de Botanique*, or Eichler, *Blüthendiagramme*.

CHAPTER XIV

INFLORESCENCE

159. Definition of inflorescence and flower cluster. The manner in which flowers are arranged on the stem is known as *inflorescence.*[1] Not infrequently the flowering shoot bears only a single flower, but very generally among seed plants these shoots are grouped into definite systems, which are called flower clusters.

160. Advantage of grouping flowers. Flowers when clustered, as in Figs. 140–143, on special nearly leafless shoots are much more conspicuous than they would be if scattered along ordinary leafy branches and partly hidden by the leaves. This is a decided advantage in securing many visits from insects which carry pollen from plant to plant (Chapter XXXII) and leads to a more abundant production of seed.


Fig. 139. Axillary and solitary flowers of pimpernel

161. Regular positions for flower buds. Flower buds, like leaf buds, occur regularly either in the axils of leaves or at the end of the stem or branch, and are therefore either *axillary* or *terminal* (Sec. 168).

162. Axillary and solitary flowers; indeterminate inflorescence. The simplest possible arrangement for flowers which arise from the axils of leaves is to have a single flower spring from each leaf axil. Fig. 139 shows how this plan appears in a plant with opposite leaves. As long as the

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[1] Sometimes (but less correctly) the word inflorescence is used to mean flower cluster.

stem continues to grow the production of new leaves may be followed by that of new flowers. Since there is no definite limit to the number of flowers which may appear in this way, the mode of flowering just described (with many others of the same general character) is known as *indeterminate inflorescence.*

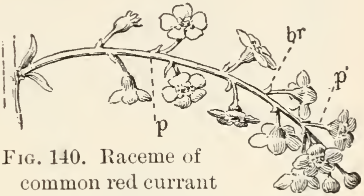

Fig. 140. Raceme of common red currant

p, peduncle; *p'*, pedicel; *br*, bract

163. The raceme and related forms. If the leaves along the stem were to become very much dwarfed and the flowers brought closer together, as they frequently are, a kind of flower cluster like that of the currant (Fig. 140) or the lily of the valley would result. Such an inflorescence is called a *raceme;* the main flower stalk is known as the *peduncle;* the little individual flower stalks are *pedicels,* and the small, more or less scale-like leaves of the peduncle are *bracts.*

Frequently the lower pedicels of a cluster on the general plan of the raceme are longer than the upper ones and make a somewhat flat-topped cluster, like that of the hawthorn, the elder, the sheep laurel, or the trumpet creeper. This is called a *corymb.*

Fig. 141. Simple umbel of cherry

In many cases, for example the parsnip, the sweet cicely, the ginseng, and the cherry, a group of pedicels of nearly equal length spring from about the same point. This produces a flower cluster called the *umbel* (Fig. 141).

164. Sessile flowers and flower clusters. Often the pedicels are wanting, or the flowers are sessile, and then a modification of the raceme is produced which is called a *spike,* like that of the plantain (Fig. 142). The willow, alder, birch, poplar, and many other common trees bear a short, flexible, rather scaly spike (Fig. 143), which is called a *catkin.*

The axis of the inflorescence is often so much shortened as to bring the flowers into a somewhat globular mass. This is called a *head* (Fig. 142). Around the base of the head usually occurs a circle of bracts known as the *involucre.* The same name is given to a set of bracts which often surround the bases of the pedicels in an umbel.

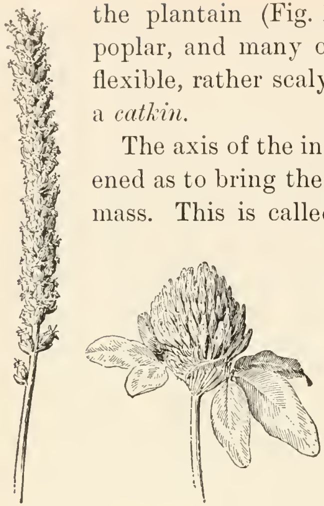

Fig. 142. Spike of plantain and head of red clover

165. The composite head. The plants of one large group — of which the dandelion, the daisy, the thistle, and the sunflower are well-known members — bear their flowers in close involucrate heads on a common receptacle. The whole cluster looks so much like a single flower that it is usually taken for one by non-botanical people. In many of the largest and most showy heads, like that of the sunflower and the daisy, there are two kinds of flowers, — the *ray flowers,* around the margin, and the tubular *disk flowers* of the interior of the head (Fig. 144). The early botanists supposed the whole flower cluster to be a single compound flower. This belief gave rise to the name of one family of plants, *Compositæ,* — that is, plants with compound flowers. In such

Fig. 143. Catkins of willow

A, staminate flowers; *B*, pistillate flowers

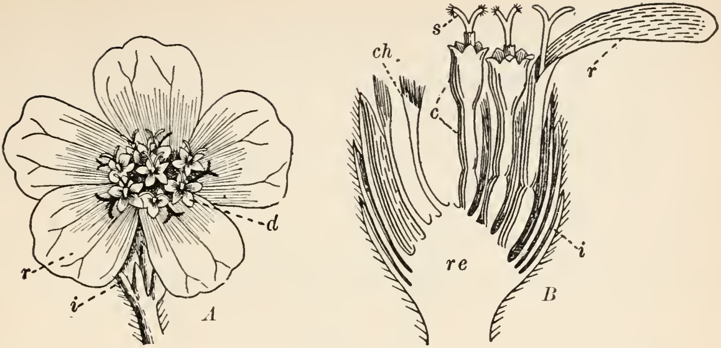

Fig. 144. Head of yarrow

A, top view (magnified); *B*, lengthwise section (magnified); *re*, receptacle; *i*, involucre; *r*, ray flowers; *d*, disk flowers; *c*, corolla; *s*, stigma; *ch*, chaff, or bracts of receptacle

Fig. 145
Panicle of oat

Fig. 146. Compound umbel
of carrot

heads as those of the tansy, the thistle, the cudweed, and the everlasting, there are no ray flowers, and in others, like those of the dandelion and the chicory, all the flowers are ray flowers.

166. Compound flower clusters. If the pedicels of a raceme branch, they may produce a compound raceme, or *panicle,* like that of the oat (Fig. 145).[1] Other forms of compound racemes have received other names.

An umbel may become compound by the branching of its flower stalks (Fig. 146), each of which then bears a little umbel, called an *umbellet.*

167. Inflorescence diagrams. The plan of inflorescence may readily be indicated by diagrams like those of Fig. 147.

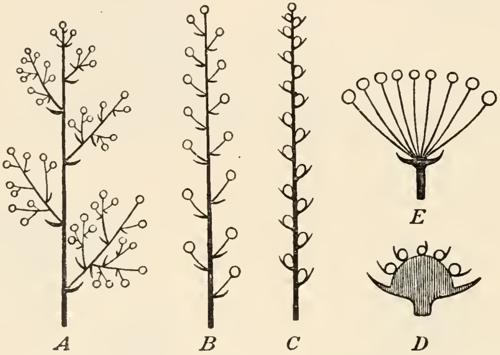

FIG. 147. Diagrams of inflorescence

A, panicle; *B*, raceme; *C*, spike; *D*, head; *E*, umbel

168. Terminal flowers; determinate inflorescence. The terminal bud of a stem may be a flower bud. In this case the direct growth of the stem is stopped or determined by the appearance of the flower; hence such plants are said to have a *determinate inflorescence.* The simplest possible case of this kind is that in which the stem bears but one flower at its summit.

169. The cyme. Very often flowers appear from lateral (axillary) buds, below the terminal flower, and thus give rise to a flower cluster called a *cyme.* This may have only three flowers, and in that case would look very much like a three-flowered

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[1] Panicles may also be formed by compound cymes (see Sec. 169).

umbel. But in the indeterminate inflorescence, such as the raceme, corymb, and umbel, the order of flowering is from below upward, or from the outside of the cluster inward, because the lowest or the outermost flowers are the oldest, while in determinate forms of inflorescence the central flower is the oldest, and therefore the order of blossoming is from the center outwards. Cymes are very commonly compound, like those of the elder and of many plants of the pink family, such as the sweet william and the mouse-ear chickweed (Fig. 148). They may also, as already mentioned, be panicled, thus making a cluster much like Fig. 147, *A*.

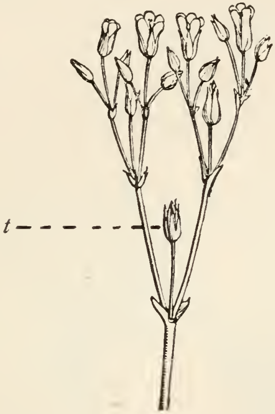

FIG. 148. Compound cyme of mouse-ear chickweed

t, the terminal (oldest) flower

CHAPTER XV

ORIGIN AND STRUCTURE OF FLORAL ORGANS; POLLINATION AND FERTILIZATION

170. The flower a shortened and greatly modified branch. In Chapter IX the leaf bud was explained as being an undeveloped branch, which in its growth would develop into a real branch (or a prolongation of the main stem). Now, since flower buds appear regularly either in the axils of leaves or as terminal buds, there is reason to regard them as of a nature similar to leaf buds. This would imply that the receptacle corresponds to the axis of the buds shown in Fig. 85, and that at least some of the parts of the flower correspond to leaves. There is plenty of evidence that this is really true. Sepals frequently look very much like leaves, and in many cactuses the bracts about the flower are so sepal-like that it is impossible to tell where the bracts end and the sepals begin (Fig. 149). The same thing is true of sepals and petals in such flowers as the white water lily. In this flower there is also a remarkable series, ranging all the

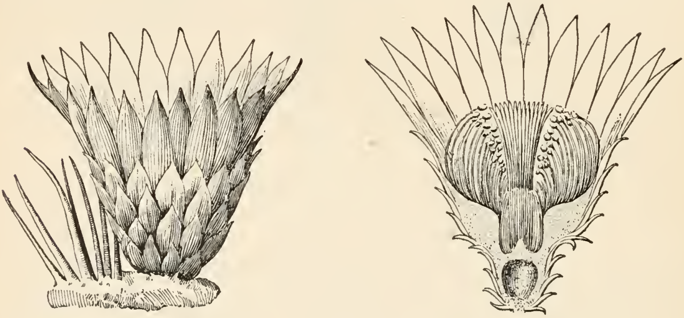

Fig. 149. Transition from bracts to sepals in a cactus flower

way from petals tipped with a bit of anther, through stamens with a broad petal-like filament, to regular stamens, as is shown in Fig. 150, *A, B, C, D*. The same thing is shown in many double roses. In completely double flowers the stamens and pistils are transformed into petals by cultivation. In the flowers of the cultivated double cherry the pistils occasionally take the form of small leaves, and some roses turn wholly into green leaves.

Summing up, then, we know that flowers are altered and shortened branches, (1) because flower buds have, as regards position, the same kind of origin as leaf buds; (2) because all the intermediate steps are found between bracts on the one hand and petals on the other.

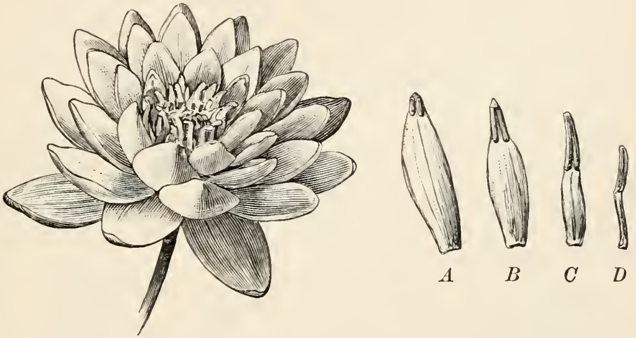

Fig. 150. Transitions from petals to stamens in white water lily

A, B, C, D, various steps between petal and stamen. — After Brown

171. Development of the anther. If the development of an anther is followed throughout, it will be found at an early stage to contain, usually, four regions, where rapid cell division is going on, which become organized into pollen sacs. These cavities (Fig. 151) are filled with pollen grains and finally merge into two pollen chambers which, in the commonest type of anther, split open lengthwise to allow the escape of the pollen.

172. Relation of stamens and carpels to structures in the lower plants. The exact significance of the stamens and carpels as organs of the plant body set apart for the purpose of reproduction can only be understood by means of a study of certain forms in the fern group, or pteridophytes; for these structures had their origin in connection with the development, from simpler conditions among the fern group, of the habit of producing seeds. The subject is treated at some length in Part II, Chapters XXVI to XXX inclusive.

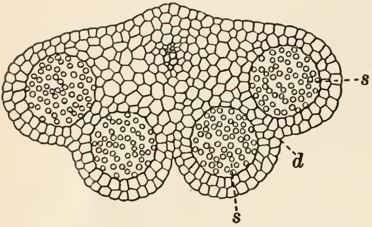

Fig. 151. Cross section of anther of mint

s, pollen sacs, with grains of pollen; *d*, groove along which the anther will split open. Somewhat magnified. — After Bonnier and Sablon

173. The anther and its contents. Some of the shapes of anthers may be learned from Figs. 129, 130, and 152.[1] The shape of the anther and the way in which it opens depend largely upon the manner in which the pollen is to be discharged and how it is carried from flower to flower. The commonest method is that in which the anther cells split lengthwise, as in Fig. 152, *A*. A few anthers open by trapdoor-like valves, as in *B*, and a larger number by little holes at the top, as in *C*.

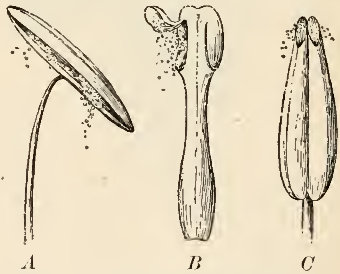

Fig. 152. Modes of discharging pollen

A, by longitudinal slits in the anther cells (amaryllis); *B*, by uplifting valves (barberry); *C*, by a pore at the top of each anther lobe (nightshade). — After Baillon

The pollen in many plants with inconspicuous flowers (as the evergreen cone-bearing trees, the grasses, rushes, and sedges) is a fine, dry powder. In plants with showy flowers it is often somewhat sticky or pasty. The forms of pollen grains are extremely various. Fig. 153 will serve to furnish examples of some of the shapes which the grains assume; *c* in that figure is perhaps as common a form as any. Each pollen grain

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[1] See Kerner and Oliver, *Natural History of Plants*, Vol. II, pp. 86–95,

consists mainly of a single cell, and is covered by a moderately thick outer wall and a thin inner one. Its contents are thickish protoplasm, full of little opaque particles and usually containing grains of starch and small drops of oil. During the germination of a pollen grain the outer coat bursts at some point, forced outward by the pressure of a tube formed from the tough inner coat. Sometimes, as in Fig. 153, *b*, there are knobs or other indications of the places at which the outer coat is most easily ruptured. After the tube has pushed its way out it continues to elongate rather rapidly.

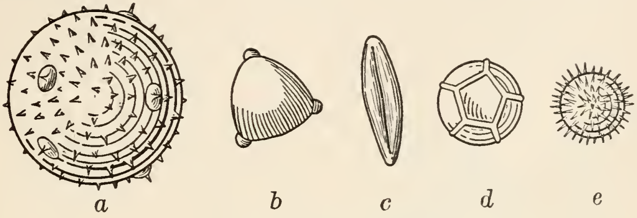

FIG. 153. Pollen grains

a, pumpkin; *b*, enchanter's nightshade; *c*, *Albuca*; *d*, pink; *e*, hibiscus. Very greatly magnified. — After Kerner

174. Microscopical structure of the stigma and style. Under a moderate power of the microscope the stigma is seen to consist of cells set irregularly over the surface, and secreting a moist liquid to which the pollen grains adhere (Fig. 154). Beneath these superficial cells is spongy parenchyma, which runs down through the style, if there is one, to the ovary. In some pistils the pollen tube proceeds through the cell walls, which it softens by means of a substance which it exudes for that purpose. In other cases (Fig. 155) there is a canal or passage along which the pollen tube travels on its way to the ovule.

FIG. 154. Stigma of thorn apple (*Datura*), with pollen

Magnified. — After Faguet

175. Pollination. The transference of pollen from anthers to stigmas is called *pollination.* In the case of plants with dry, dust-like pollen this is generally due to the action of the wind. Moist, sticky pollen is generally carried by some kind of animal, usually by insects. The subject of pollination is so important, especially in relation to the visits of insects, that it needs a chapter by itself (see Chapter XXXII).

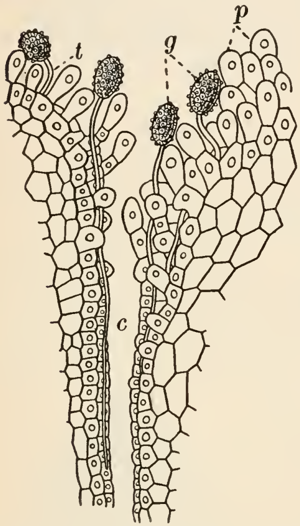

Fig. 155. Pollen grains producing tubes, on stigma of a lily

g, pollen grains; *t*, pollen tubes; *p*, papillæ of stigma; *c*, canal or passage running toward ovary. Much magnified.—After Dodel-Port

176. Fertilization. By *fertilization* in seed plants the botanist means the union of a male sexual nucleus from a pollen grain with the female nucleus of the egg cell at the apex of the embryo sac (Fig. 157). This process gives rise to a cell which contains protoplasm derived from the pollen tube and from the egg cell. In many plants the pollen, in order best to secure fertilization, must come from another plant of the same kind, and not from the individual which bears the ovules to be fertilized.

Pollen tubes (Fig. 156) begin to form soon after pollen grains lodge on the stigma. The time required for the process to begin varies in different kinds of plants, requiring in many cases twenty-four hours or more. The length of time needed for the pollen tube to make its way through the style to the ovary depends upon the length of the style and other conditions. In the crocus, which has a style several inches long, the descent takes from one to three days.

Finally the tube penetrates the opening at the apex of the ovule (Fig. 157, *m*), called the *micropyle* (meaning little gate), and transfers a male nucleus into the egg cell.

177. Nature of the fertilizing process. The necessary feature of the process of fertilization is *the union of the essential contents of two cells, especially the nuclei, to form a new one from which the future plant is to spring.* This kind of union also occurs in all the lower plants (Chapters XX–XXXI), resulting in the formation of a spore capable of growing into a complete plant like that which produced it. It is a sexual act and can be studied much better in some of the algæ, mosses, and ferns than in seed plants.

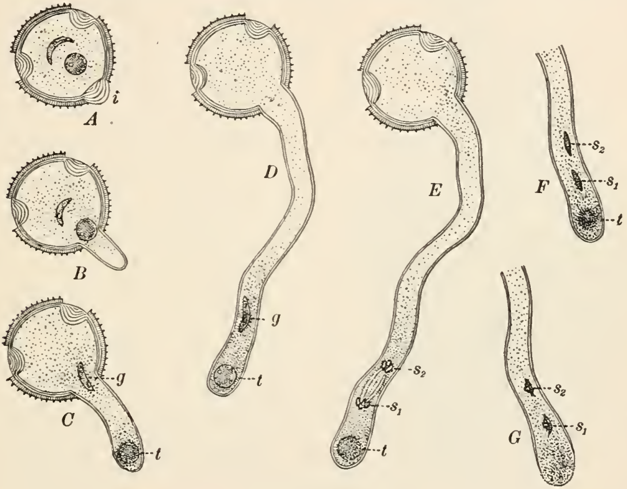

FIG. 156. Germination of the pollen grain of an angiosperm

A, inner coat of the pollen grain distended by osmosis from contact with the moist stigma, and protruding slightly at the point *i*; *B*, the pollen tube beginning to form; *C*, the pollen tube more elongated, with the tube nucleus *t* at its tip, the generative cell *g* having begun to enter the tube; *D*, the pollen tube still farther elongated; *E*, the division of the nucleus of the generative cell to form the two sperm nuclei s_1 and s_2; *F*, the sperm cells s_1 and s_2 fully formed, and the tube nucleus *t* breaking down; *G*, the tube nucleus has disappeared, and the sperm cells are about to be discharged near the tip of the pollen tube. Somewhat diagrammatic and much magnified. — After Bonnier and Sablon

178. Development of the embryo. After fertilization the egg cell finally develops the embryo of the future seed. This formation of the embryo is always a complicated process and varies much in different groups of seed plants. Briefly stated, the process in angiosperms is as follows. The egg cell (Fig. 158, *A*) some time after fertilization forms a transverse partition and is thus divided into two cells, one of which (Fig. 158, *B*, *s*) is to form the slender *suspensor* of the embryo (which serves various purposes, such as forcing the embryo into the nutritive tissue of the seed, absorbing food from the wall of the ovary, or storing food for the growing embryo) and the other (*e*) is to form the embryo itself. These cells in turn subdivide, as shown in *C*, *D*, and *E*. The whole pear-shaped body in parts *B–E* is called the *pro-embryo*, and this continues to grow and its cells to subdivide until its structure becomes highly complex. Finally it contains many sharply defined regions which gradually develop into the several organs of the full-grown embryo.

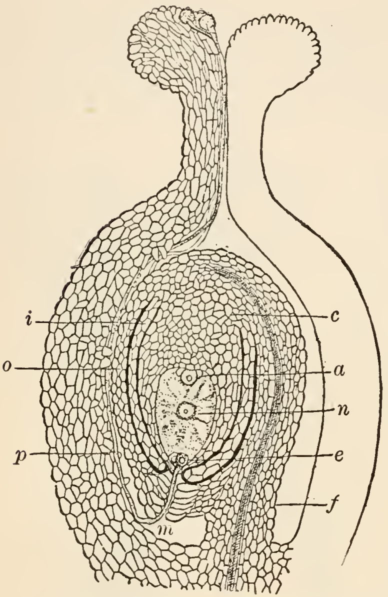

Fig. 157. Diagrammatic representation of fertilization of an ovule

i, inner coating of ovule; *o*, outer coating of ovule; *p*, pollen tube proceeding from one of the pollen grains on the stigma; *c*, the place where the two coats of the ovule blend. (The kind of ovule here shown is inverted, its opening *m* being at the bottom, and the stalk *f* adhering along one side of the ovule.) *a* to *e*, embryo sac, full of protoplasm; *a*, so-called antipodal cells of embryo sac; *n*, central nucleus of the embryo sac; *e*, nucleated cells, one of which, the egg cell, receives the male nucleus of the pollen tube; *f*, funiculus or stalk of ovule; *m*, micropyle or opening into the ovule. — After Luerssen

179. Number of pollen grains to each ovule. Only one pollen grain is necessary to fertilize each ovule, but so many pollen grains are lost that plants produce many more of them than they do ovules. The ratio, however, varies greatly. In the night-blooming cereus there are about 250,000 pollen grains for 30,000 ovules, or rather more than 8 to 1; in the common garden wistaria there are about 7000 pollen grains to every ovule, and in Indian corn, the cone-bearing evergreens, and a multitude of other plants, there are many times more than 7000 to 1. These differences depend upon the mode in which the pollen is carried from the stamens to the pistil. Plants which are pollinated by the wind must produce far more pollen, to allow for inevitable waste, than those which are self-pollinated, or pollinated by insects (Chapter XXXII).

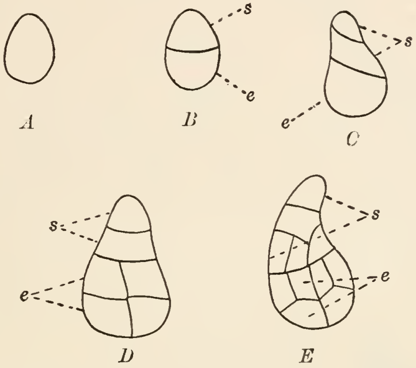

FIG. 158. First stages in the development of the egg cell of the European ivy (*Hedera Helix*)

A, egg cell. *B*: *s*, cell which will form the suspensor; *e*, cell which will form the embryo. *C*, showing first subdivision of the suspensor-forming cell; *D*, showing subdivision of the embryo-forming cell; *E*, showing subdivision of both regions, slightly more advanced. — After Bonnier and Sablon

CHAPTER XVI

THE FRUIT[1]

180. What constitutes a fruit. It is not easy to make a short and simple definition of what botanists mean by the term *fruit.* It has very little to do with the popular use of the word. Briefly stated, the definition may be given as follows: *The fruit of a seed plant consists of the matured ovary and contents, together with any intimately connected parts.* Botanically speaking, the bur of beggar's ticks (Fig. 344), the three-cornered grain of buckwheat, and such true grains as wheat and oats are as much fruits as is an apple or a peach.

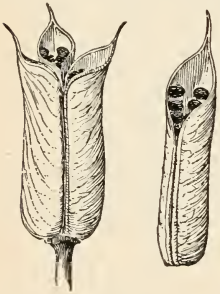

FIG. 159. Group of follicles and a single follicle of the monkshood

After Faguet

181. Classes of fruits. Fruits may be divided into four classes as follows: (*a*) *unipistillary fruits,* those which result from the ripening of a single pistil; (*b*) *aggregate fruits,* those which result from the ripening of a cluster of carpels of one flower, massed together; (*c*) *accessory fruits,* those in which the main bulk of the fruit consists of something else besides the carpels,— e.g. calyx or receptacle, — added to a simple or an aggregate fruit; (*d*) *multiple or collective fruits,* those which result from the combination of the ripened pistils of two or more flowers into one mass.

182. Forms of unipistillary fruits: the capsule. This is a dry fruit, splitting open (*dehiscing*) to allow the seeds to escape. Capsules of simple pistils may either open along one line, as

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[1] See Gray, *Structural Botany*, chap. vii, also Kerner and Oliver, *Natural History of Plants*, Vol. II, pp. 227–438.

in the *follicles* of monkshood (Fig. 159), or along two lines, as in the *legumes* of the pea (Fig. 343). Many capsules result from the ripening of compound pistils, as the poppy, *Datura*, or jimson weed (Fig. 343), and crocus (Fig. 166, I, *B*).

The schizocarp. This is a dry fruit, breaking into pieces which do not split open, the name meaning breaking fruit (Figs. 160, 166, II).

The akene, grain, and nut. These are dry fruits which never split open (indehiscent fruits).

Under the general name *akene* are grouped several types of fruits. Many, like those of Fig. 161, are small one-seeded carpels. Another large group, the fruits of the family *Compositæ*, has akenes which result from the ripening of an inferior ovary, frequently crowned by the limb of the calyx (Fig. 166, III).

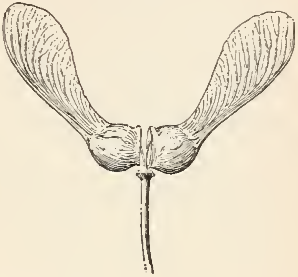

Fig. 160. Schizocarp of maple
After Faguet

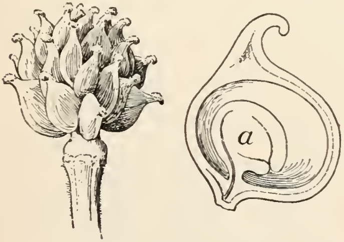

Fig. 161. Akenes of a buttercup

A, head of akenes; *B*, section of a single akene (magnified); *a*, seed

Fig. 162. Chestnuts

Grains, such as corn, wheat, oats, barley, rice, and so on, have the interior of the ovary completely filled by the seed, and the seed coats and the wall of the ovary are firmly united, as shown in Fig. 3. Naturally, therefore, they are popularly supposed to be seeds and are always so called by non-botanical people.

A nut (Fig. 162) is larger than an akene, usually has a harder shell, and commonly contains a seed which springs from a single ovule in one locule of a compound ovary, which develops at the expense of all the other ovules. The chestnut bur is a kind of involucre, and so is the acorn cup. The name *nut* is often incorrectly applied in popular language; for example, the "Brazil nut" is really a large seed with a very hard testa.

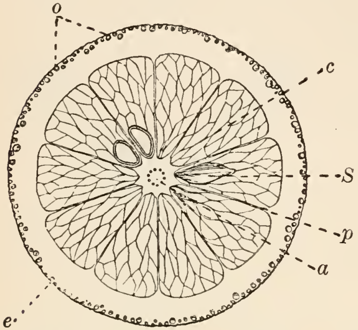

Fig. 163. Cross section of an orange

a, axis of fruit, with dots showing cut-off ends of fibro-vascular bundles; *p*, partition between cells of ovary; *S*, seed; *c*, locule of ovary filled with a pulp composed of irregular sacs full of juice; *o*, oil reservoirs near outer surface of rind; *e*, corky layer of epidermis. — After Decaisne

183. The berry. This is a generally fleshy fruit, which usually does not split open. Such berries as the tomato, grape, and persimmon result from the ripening of a superior ovary. Those of the gooseberry, currant, and many others result from half-inferior or inferior ovaries, and therefore a considerable part of the bulk of the fruit is receptacle. The leathery-skinned fruit of the orange family is a true berry.

The fruit of the apple, pear, and quince is called a *pome*. It consists of a several-loculed ovary, — the seeds and the tough membrane surrounding them in the *core*, — inclosed by a fleshy edible portion which makes up the main bulk of the fruit. In the apple and the pear much of the fruit is receptacle.

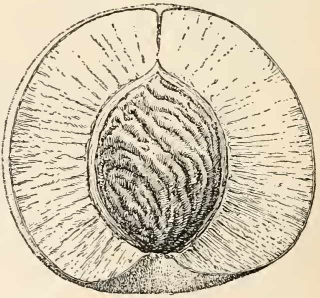

Fig. 164. Peach. Longitudinal section of drupe

After Decaisne

In the squash, pumpkin, and cucumber the ripened ovary, together with the receptacle, makes up a peculiar fruit (with a firm outer rind) known as the *pepo.* The relative bulk of the greatly enlarged hollow receptacle and of the ovary in such fruits is not always the same.

The drupe. This fruit is often fleshy, and usually does not split open. The *pericarp,* or wall of the ripened ovary (meaning round about and fruit), consists of an outer fleshy (or fibrous or leathery) layer, the *exocarp,* and an inner, somewhat hard or stony layer, the *endocarp.* In common language the endocarp with its contained seed is called a "stone"; hence drupes are often known as stone fruits. Most drupes, as in the case of the peach (Fig. 164), cherry, plum, cocoanut, and walnut, are one-stoned and one-seeded.

FIG. 165

A, strawberry; *B*, raspberry; *C*, mulberry. — After Faguet

184. Aggregate fruits. The raspberry (Fig. 165, *B*), blackberry, and similar fruits consist of many carpels, each of which ripens into a part of a compound mass which, for a time at least, clings to the receptacle. The whole is called an *aggregate fruit.*

185. Accessory fruits. Not infrequently, as in the strawberry (Fig. 165, *A*), the main bulk of the so-called "fruit" consists rather of the receptacle than of the ripened ovary or its appendages. Such a combination is called an *accessory fruit.*

186. Multiple fruits. The fruits of two or more flowers may blend into a single mass, known as a *multiple fruit.* Perhaps the best-known edible examples of multiple fruits are the mulberry (Fig. 165, *C*) and the pineapple. The last-named fruit is an excellent instance of the seedless condition which often results from long-continued cultivation.

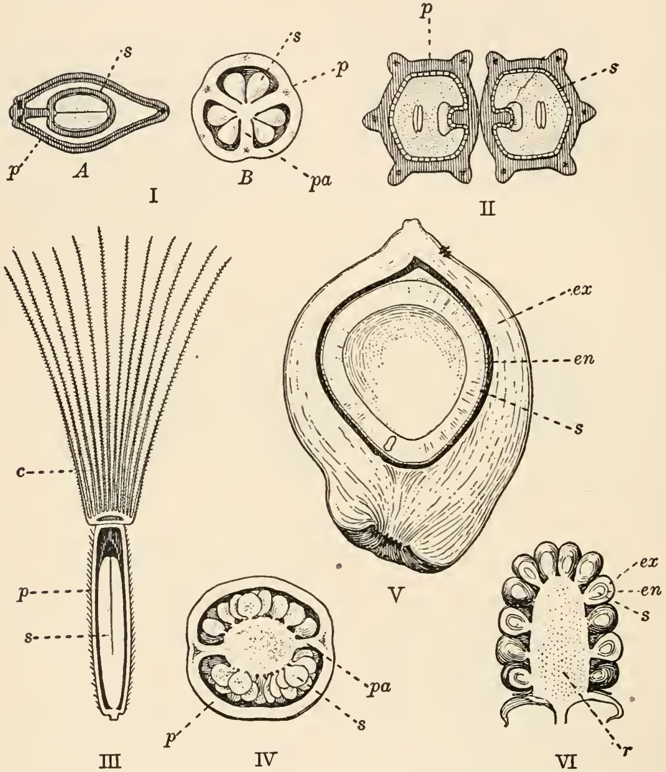

Fig. 166. Comparative sections of fruits

I, capsule: *A*, unilocular liquorice pod, cross section (magnified); *B*, trilocular crocus pod, cross section (magnified). II, schizocarp, double fruit of poison hemlock (*Conium*), cross section (magnified); III, akene of arnica, longitudinal section (magnified); IV, berry of pepper (*Capsicum*), cross section (reduced); V, drupe of cocoanut, longitudinal section (reduced); VI, aggregate and accessory fruit of blackberry, longitudinal section (reduced). — I–IV, after Schmidt; V, after Decaisne; VI, (modified) after Gray

c, limb of calyx; *en*, endocarp; *ex*, exocarp; *p*, pericarp; *pa*, partition between locules; *r*, receptacle; *s*, seed

PART II

THE MORPHOLOGY, EVOLUTION, AND CLASSIFICATION OF PLANTS

CHAPTER XVII

THE PRINCIPLES OF MORPHOLOGY, EVOLUTION, AND CLASSIFICATION

187. Morphology. *Morphology* treats of the form and structure of a plant or animal. The lowest organisms have a simple morphology, but the higher plants and animals are made up of many parts or *organs,* and consequently their morphology is very complex. Organs are structures set apart or developed for a definite kind of work. Thus the roots of a plant are organs usually employed to attach the plant to the ground in order that it may absorb soil moisture.

One department of morphology (comparative morphology) deals with the various forms or disguises which the same sort of organ may take in different kinds of plants, and compares these structures with one another. For example, the foliage leaf is a well-defined organ which can be recognized at a glance; but it requires some study to understand that the scales on the bud and around an onion, and also some forms of spines and tendrils are morphologically leaves, that is are leaves variously modified. Because all of these structures are related to one another they are called *homologous,* and morphology studies the *homologies,* or relationships, of organs. Comparative morphology is one of the most interesting subjects of biological study, since it furnishes the basis for the established belief in the evolution or development of the higher plants and animals from simpler forms.

188. Classification. The *classifications* of animals and plants are attempts to express the actual kinships, or what among human beings are called blood relationships, which are believed to exist among them. To illustrate the principles of classification let us consider the position of the pines among plants. All of the pines have for their fruit a scaly *cone* whose seeds are borne *naked* at the base of each scale and mature the *second* year. The leaves are *needle-shaped, evergreen,* and *clustered.* Any tree which has all the characteristics above given is a pine.

The spruces, hemlocks, firs, and larches agree with the pines in many respects, but all of them mature their seeds the first year, and their foliage is different. The American cypress has a globular woody cone and deciduous leaves in two rows. The arbor vitæ and the juniper have awl-shaped or scale-like leaves, not in clusters.

All of these cone-bearing trees are distinct kinds, but they are grouped together because the seeds are borne *naked* on the scales of the cones. This peculiarity separates the group from a much larger assemblage of seed plants in which the seeds are borne *inclosed* in seed cases, pods, or other types of fruit. Finally, all of the *seed*-bearing plants are separated from the *spore*-bearing groups by the possession of methods of reproduction which develop *seeds.*

Thus the pines find their place in the classification of plants through clearly marked characters which define several different groups. These characters are (1) the presence of the seed, (2) the fact that the seeds are exposed or naked, (3) the development of the seeds in a cone type of fruit, and finally (4) some peculiarities of the cone, and the character of the foliage. The process of classification leads from an assemblage of more than one hundred thousand kinds of plants (the seed plants), through successively smaller divisions, to the relatively small group of the pines, with hardly more than seventy known kinds.

189. Nomenclature. It was long ago found convenient to give Latin names to the kinds of animals and plants and to their various natural groups. These names constitute the *nomenclature* of botany and zoölogy. Each kind of plant or animal is termed a *species.* A group of closely related species constitutes a *genus* (plural, *genera*). Every species is given a name that consists of two parts. There is the specific name, which defines the species, and the generic name, which includes the more immediate relatives. The specific name follows the generic, just as the first name of a man follows his family name or his surname in a directory. Furthermore, an abbreviation of the name of the botanist who first described the species follows the combination of generic and specific names. Thus the name of the pitch pine is written *Pinus rigida* Mill., this species having been described by a botanist named Miller. This universally adopted system of designating species by two names, known as the binomial system of nomenclature, was perfected by the famous Swedish naturalist Linnæus, and the edition of his *Species Plantarum,* which is the basis of all botanical classification, bears the date 1753.

Closely related genera are grouped into *families,* whose names generally terminate in the ending *-aceæ,* and families are brought together into *orders,* whose names are written with the uniform ending *-ales.* Orders are further assembled into *classes,* and the classes into *subdivisions,* or more frequently into *divisions,* of the plant kingdom. Applying this system of classification, we have all the species of pines in the genus *Pinus,* in the family *Pinaceæ,* in the order *Coniferales,* in the class *Coniferæ,* in the subdivision *Gymnospermæ* of that highest division of the plant kingdom, the *Spermatophyta.*

190. Organic evolution. In the times of Linnæus, who lived in the eighteenth century, almost all naturalists believed that the species or kinds of animals and plants had never changed in their characters during their long history on the earth. They believed that new kinds could only arise by special acts of creation. This doctrine of special creation gave way to the present belief in *organic evolution*, or the *theory of descent*, chiefly through the work of Charles Darwin, whose famous book, *The Origin of Species*, appeared in 1859. The theories of organic evolution hold that all the existing species of animals and plants have been derived or evolved through the geological ages from the simplest forms of life in the beginning. These theories also hold that the kinds now on the earth are subject to change, and that very many of them are in process of developing new species. There are varying opinions as to the causes which bring about changes in species, and there are several schools of evolutionists whose theories are the subject of constant discussion and investigation.[1] But all botanists and zoölogists believe in the main principles of organic evolution; and the theory is the framework of biology. Indeed, the theory of organic evolution is as important to biology as the atomic theory is to chemistry and as the doctrine of the conservation of energy is to physics.

191. An outline of the classification of plants. We shall present at this point a classified arrangement of the most important of the larger groups of plants. It is quite impossible to develop a classification very far in the compass of this book, but this outline will serve to indicate the field covered in the succeeding chapters.[2] The thallophytes are especially difficult to classify, for the groups are not as clearly understood as those of the higher plants, and there are complex relationships, especially between the algæ and the fungi. The classification of the green algæ offers exceptionally difficult problems, and the arrangement presented here is largely one of convenience in the present state of our knowledge of this puzzling assemblage of forms. Classifications are, of course, subject to constant modification, as groups receive more and more careful study, and authors frequently differ widely in their systems.

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[1] See Chapter XXXIX, Variation, Mutation, and Origin of Species.

[2] For the most recent and detailed classification of plants the reader is referred to Engler, *Syllabus der Pflanzenfamilien*, 1903, or to Engler and Prantl, *Die Natürlichen Pflanzenfamilien.*

AN OUTLINE OF THE CLASSIFICATION OF PLANTS

Division I. *Thallophyta*, the thallus plants, or thallophytes.

- Series of the Algæ.
  - Class I. *Cyanophyceæ*, the blue-green algæ.
  - II. *Chlorophyceæ*, the green algæ.
    - Order 1. *Protococcales*, the one-celled green algæ.
    - 2. *Confervales*, the confervas and sea lettuce.
    - 3. *Conjugales*, the pond scums
    - 4. *Diatomales*, the diatoms.
    - 5. *Siphonales*, the siphon algæ.
    - 6. *Charales*, the stoneworts.
  - III. *Phæophyceæ*, the brown algæ.
  - IV. *Rhodophyceæ*, the red algæ.
- Series of the Fungi.
  - Class V. *Schizomycetes*, the bacteria.
  - VI. *Saccharomycetes*, the yeasts.
  - VII. *Phycomycetes*, the alga-like fungi.
  - VIII. *Ascomycetes*, the sac fungi.
  - IX. *Basidiomycetes*, the basidia fungi.

Division II. *Bryophyta*, the liverworts and mosses, or bryophytes.

- Class I. *Hepaticæ*, the liverworts.
  - Order 1. *Ricciales*, the *Riccia* forms.
  - 2. *Marchantiales*, the *Marchantia* forms.
  - 3. *Jungermanniales*, the *Jungermannia* forms, or leafy liverworts.
  - 4. *Anthocerotales*, the *Anthoceros* forms.
- II. *Musci*, the mosses.
  - Order 1. *Sphagnales*, the peat mosses.
  - 2. *Bryales*, the common mosses.

Division III. *Pteridophyta*, the ferns and their allies, or pteridophytes.

- Class I. *Filicineæ*, the true ferns.
- II. *Equisetineæ*, the horsetails.
- III. *Lycopodineæ*, the club mosses.

Division IV. *Spermatophyta*, the seed plants, or spermatophytes.

- Subdivision I. *Gymnospermæ*, the gymnosperms.
- II. *Angiospermæ*, the angiosperms.[1]
  - Class I. *Monocotyledoneæ*, the monocotyledons.
  - II. *Dicotyledoneæ*, the dicotyledons.

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[1] The reader should note that in this classification the angiosperms contain only two out of sixteen classes of somewhat equivalent value.

CHAPTER XVIII

THE LOWEST ORGANISMS AND THE CELL AS THE LIFE UNIT

192. The process of evolution. The higher complex animals and plants are readily distinguished from one another, but the differences become less apparent in the lower, simpler forms. There are indeed groups of uncertain position, some authors placing them among the plants and some among the animals.

The animal and plant kingdoms, in the process of evolution, followed a tree-like method of development. The forms and groups split up into divergent lines which constantly gave off, and are still giving off, new shoots. Thus from a number of trunks in the beginning there have been derived a multitude of smaller branches, and from these in turn have arisen countless twigs. It is impossible to construct accurately these genealogical trees, because the species now living occupy the position of buds on the structure, some relatively low down and some at the highest points, but *all* at the *ends* of their respective lines of development. The forms which represented the lowest and intermediate stages of development are almost all extinct,— that is, have long ago died out on the earth, — and we can only judge of their structure by the fragmentary remains which are left as fossils, or by comparative studies on the structure and development of living species, which frequently give us suggestions of what took place in the long process of organic evolution.

193. The simplest living unit a cell. The living material of organisms, that is the part which possesses life, is called *protoplasm.* Protoplasm is not a simple substance, but, on the contrary, is the most involved mixture of the most complex substances which the chemist knows. These belong to the group called *proteids,* a familiar example of which is the white of egg (albumen). Very little is known of the exact chemical structure of the numerous proteids. Their molecules are very complex, for they contain a large number of elements of remarkably varied chemical properties, — carbon, nitrogen, oxygen, hydrogen, sulphur, and in some cases phosphorus. But besides the proteids and many other *organic* compounds (substances usually formed only in association with life processes, as, for example, the sugars, starch, and fats), protoplasm also contains certain necessary *inorganic* substances, such as salts of sodium, potassium, calcium, magnesium, and iron, and in addition to these a very large amount of water.

Although we know very little about the chemical nature of protoplasm, certain remarkable structural peculiarities have been recognized for a long time. Protoplasm always exists in the form of units which are called *cells.* The simplest organisms consist of solitary units, and are consequently termed *one-celled* (unicellular). The higher organisms are made up of aggregates of cells, and are termed *many-celled* (multicellular).

The cells in many-celled organisms have each a separate individuality, but they are usually set apart for particular kinds of work and depend upon one another for mutual assistance. The many-celled organism has been termed a *cell republic,* because all the cells, as individuals, work for the common good of the community, and by a system of helpful division of labor benefit one another.

There is a large group of one-celled microscopic animals called the *Protozoa.* This constitutes the lowest division of the animal kingdom, and is quite distinct from the groups of many-celled animals, although they are believed to have been derived from it. There are likewise numerous one-celled plants, but they are related to the higher many-celled forms by very complete and interesting connecting links, so that botanists do not make a group of one-celled plants, and can readily understand the evolution of the many-celled forms from the single-celled.

It is much easier to understand the structure of the plant cell by comparing it with one of the simplest of the one-celled animals; so at this point there will be given a brief account of one of the best-known protozoans, the *Amœba*.

194. The Amœba.* The *Amœba* under the microscope appears as a minute, irregularly shaped body of a jelly-like consistency. Its form when active constantly changes. A finger-like extension or process is thrust out from one side (Fig. 167, *A*) and the somewhat granular protoplasm flows into this from neighboring regions. Other processes are successively withdrawn, so that the protoplasm actually moves or flows slowly forward into the newly formed lobe, and thus the *Amœba* glides along. There is present in the protoplasm a denser protoplasmic structure termed the *nucleus*, which is known to be the center of very important activities in the cell. The protoplasm also contains numerous small granules, and frequently large food particles, and there are also globules, called *vacuoles*, of a watery fluid, which appear and disappear in the thicker substance. Such is the structure of a typical cell, which may be defined as *a small mass of protoplasm containing a nucleus*.

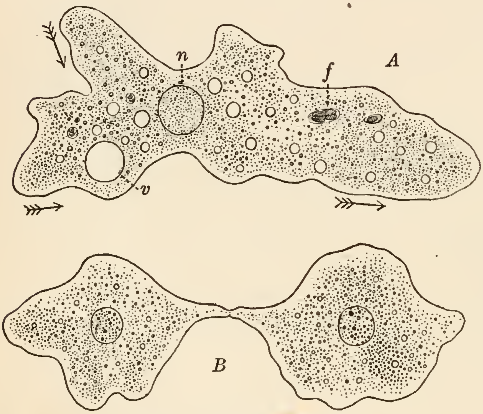

FIG. 167. The *Amœba*

A, an individual moving in the direction of the arrows; *n*, nucleus; *v*, pulsating vacuole; *f*, food body. *B*, the process of cell division by constriction, a nucleus in each half. — *B*, after Jordan, Kellogg, and Heath

* TO THE INSTRUCTOR: If material of *Amœba* is available, its study will furnish an excellent introduction or accompaniment to laboratory work on the plant cell.

The *Amœba* feeds upon smaller organisms. These may be drawn in at any point on the surface of the cell, whose protoplasm simply flows around the bodies and thus takes them into the interior. The oxygen gas held in the water which bathes the *Amœba* is also absorbed all over its surface. Food materials which cannot be digested, together with the waste products, are left behind by the protoplasm as it moves from place to place.

When the *Amœba* reaches a certain size there takes place the interesting event called *cell division.* The cell divides, by a process of constriction (Fig. 167, *B*), into similar halves, which separate from one another as two independent daughter *Amœbæ.* Previous to the division of the cell there has been a division of the nucleus, so that each daughter *Amœba* is provided with a daughter nucleus, and therefore has exactly the same structure as the parent cell, but is, of course, only about half as large. Cell division is the method of cell reproduction. It is interesting to note that in this process of reproduction there has been no loss of protoplasm, no death of any region of the parent *Amœba*, but from the division of one have come two. There is, therefore, no death from old age in one-celled organisms. They are being killed constantly, of course, by adverse conditions, or eaten by other animals. These are the accidents of life. However, the *Amœba* and other one-celled animals and plants need never die of old age; that is, there is nothing in the constitution of such an organism to prevent its living forever.

195. The plant cell. The plant cell generally differs from the animal cell in two important respects.

First. The protoplasm is inclosed in a little box-like chamber with transparent walls. The substance of the walls is called *cellulose,* — a compound belonging to the great group of the starches and sugars (carbohydrates). Such an envelope is termed a *cell wall;* and is peculiar to plants. Indeed, the term *cells,* as used in biology, was first applied to the chambers inclosed by cell walls, which may be seen in thin sections of cork, pith, and other plant structures.

Second. The protoplasm of green portions of plants will be found to contain green bodies called *chromatophores* (meaning color bearers). Chromatophores have a great variety of forms in different plants and are sometimes very complex and beautiful, — as the spiral band in the cells of the pond scum, *Spirogyra* (Fig. 168, *A*). The green coloring matter in a chromatophore is called *chlorophyll* (meaning leaf green). Green chromatophores are called *chloroplasts* when small and numerous in a cell. Chloroplasts are characteristic of the cells in plants above the thallophytes, and may be readily studied in the leaves of mosses (Fig. 169, *A*), ferns, and seed plants. Chromatophores are sometimes colored brown or red, as in the cells of the brown and the red algæ. Chromatophores are peculiar to plants, never being found in typical animal cells.

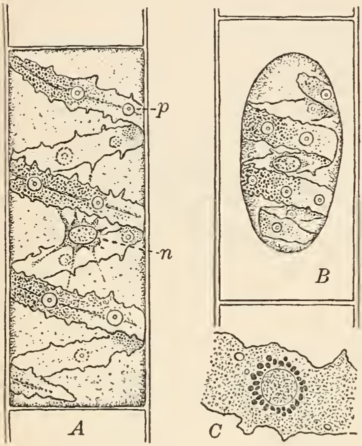

FIG. 168. Cell structure of the pond scum (*Spirogyra*)

A, living cell, showing spiral band-like chromatophore with pyrenoids *p*, and centrally placed nucleus *n*; *B*, living cell after treatment with a salt solution, the protoplasm contracted away from the cell wall; *C*, pyrenoid stained with iodine and very greatly magnified (about 1000 diameters), a circle of starch grains around the pyrenoid

The protoplasm of the plant cell always lies directly under the cell wall, sometimes completely filling the cavity, but more frequently forming a lining which surrounds one or more spaces, or vacuoles, which contain a watery fluid called *cell sap*. The relation of the protoplasm to the cell wall is easily understood when the protoplasm is made to contract from the wall by the withdrawal of the watery cell sap from the vacuoles. Thus if a filament of a pond scum or a portion of a moss leaf be placed in an aqueous solution of common salt (5 or 10 per cent), the cell sap is drawn out of the vacuole (osmotically) and the bounding layer of protoplasm shrinks away from the wall (Figs. 168, *B*; 169, *B*). The force that keeps the layer of protoplasm against the cell wall is called *cell turgor*.

The mass of protoplasm inclosed by the cell wall is called the *protoplast*, and always contains at least one nucleus. Some plant cells have many nuclei. The position of the nucleus is somewhat variable. In the cell of the pond scum (Fig. 168, *A*, *n*) it is situated in the middle region and held in place by delicate strands of protoplasm which run out to the protoplasmic layer under the cell wall, but the nucleus frequently lies just under the wall, as in the moss leaf (Fig. 169, *A*, *n*). The chromatophores are generally found in the outer layer of protoplasm under the cell wall. There are also many granules in the protoplasm, some of them minute globules of oils and fats and others of a proteid character. Many of these are food products in the cell. Finally, the central portion of the cell generally contains a single vacuole filled with cell sap.

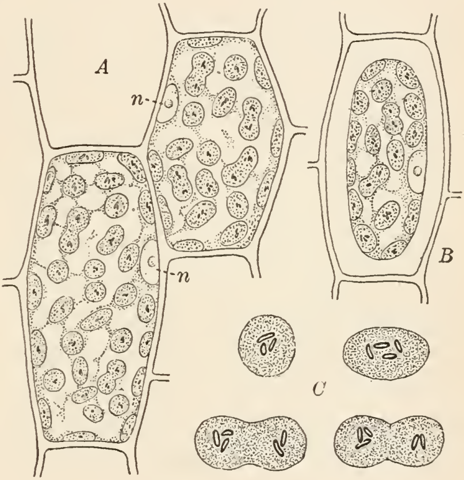

Fig. 169. Cell structure of the moss leaf (*Funaria*)

A, two living cells from a leaf, showing the numerous chloroplasts and the position of the nucleus *n* in the layer of protoplasm under the cell wall; *B*, living cell after treatment with a salt solution, the protoplast contracted away from the cell wall; *C*, stages illustrating the division of the plastids, starch grains shown in their interiors

It is clear that the protoplast of the plant cell corresponds to the entire *Amœba* or any other animal cell. The cell wall is a formation outside of the protoplast and is not a living part of the plant cell. Many lower plants form reproductive cells (zoöspores, gametes, etc.), which for some time are without a cellulose wall, and in this condition are motile and behave like animal cells. However, the cell walls and the chromatophores are responsible for the most conspicuous differences between plants and animals, as is noted in Sec. 202.

196. Photosynthesis.[1] Chromatophores and chloroplasts in the presence of sunlight are able to manufacture from water and the simple gas carbon dioxide certain complex organic foods of which starch is generally the first visible product. This process is called *photosynthesis*, which signifies a putting together by light. The chemical formula for carbon dioxide is CO_2, for water H_2O, and for starch $C_6H_{10}O_5$. The chemistry of the manufacture of starch cannot be truthfully shown by a simple equation, for starch is not formed directly from carbon dioxide and water, but by several steps through invisible substances that have not been isolated and therefore have never been studied. The chemical processes in these steps are not well understood. The final results may be roughly expressed as follows:

$$6\,CO_2 + 5\,H_2O = C_6H_{10}O_5 + 6\,O_2.$$

This shows why free oxygen is formed during the processes of photosynthesis. In some plants starch is never manufactured, but instead sugars, which are substances closely related to starch, some of them having the formula $C_6H_{12}O_6$. The sugars are in solution and invisible. Oil is formed in some plants, as in the green felt (*Vaucheria*), diatoms, etc., in place of starch, as the first visible product of photosynthesis.

Many chromatophores have well-defined denser regions called *pyrenoids*, which are the centers of starch formation, as is well illustrated in the pond scum (Fig. 168, *C*). Chloroplasts

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[1] The subject of photosynthesis is treated in greater detail in connection with the structure and functions of leaves (Chapter XII), especially in Secs. 127–132.

frequently contain starch grains, as may be readily shown in the cells of the moss leaf (Fig. 169, *C*) when colored (stained) with iodine. Photosynthesis is only found in plants containing chlorophyll or other pigments of a similar physiological nature. The sun furnishes the energy in the form of light for the building up of the simplest food products, and the plant cell is the main factory which supplies the food of the world.

197. The food of plants; assimilation. All plants with chlorophyll can manufacture their own food by the processes of photosynthesis. Moreover, it is manufactured directly within the protoplasm of the cell and does not have to be absorbed from without, as in the case of the animal cell (see account of *Amœba*, Sec. 194).

As we have already noted, starch is generally the first visible product of this process of food manufacture (photosynthesis). Starch and the related substances, sugars, are the primary foods of green plants, and the most important, but they are merely the starting point for a complex series of processes through which the highly organized proteids of the protoplasm are derived. There are some plants which lack chlorophyll, as the fungi and certain plant parasites, and they, like the animals, depend upon food absorbed from without the body. The food of plants is broken down and recombined in various ways to form the protoplasm, as it is in animals, and the breaking down of some of the substances sets free energy in the form of plant heat (corresponding to animal heat), as is easily proved in the germination of seeds (see Sec. 5). So the processes of food absorption, or *assimilation*, in plants are essentially the same as in animals, but the manufacture of food (photosynthesis) is an entirely different process and peculiar to plants.

198. The food cycle. There is a circulation of certain elements (especially carbon, nitrogen, sulphur, and phosphorus) through the bodies of plants and animals which may be called the food cycle (see diagram, Fig. 207). It begins in the plant cell with the manufacture of starch, and related substances (carbohydrates) by photosynthesis. This makes carbon, obtained from the carbon dioxide of the air, available in these primary foods. Nitrogen is obtained from the nitrates dissolved in water and drawn up through the roots, and sulphur and phosphorus in a similar manner from sulphates and phosphates. The proteids of protoplasm are built up from these elements, with the addition of hydrogen and oxygen. Plants are able to form some very complex organic substances, but animals are able to carry the building-up process still farther, for the highest forms of proteids known are found in their substance.

There is, however, a turning point in the building-up activities when complex compounds begin to break down into simpler substances. Some of these are the daily waste products of an animal or plant. The most striking phenomena are those which occur during the processes of decay, which begin at once with the death of an organism. Decay is the process by which highly complex organic compounds are broken down into successively simpler substances. The final steps return the elements carbon, nitrogen, sulphur, and phosphorus to the earth and air in very simple forms available again for the constructive work of green plants. The processes of decay are due to the growth and activities of bacteria and other fungi, and the subject is treated at some length in Sec. 252.

199. Cell division, growth, and reproduction. Assimilation increases the amount of protoplasm, and this results in growth and reproduction through cell and nuclear division. Cell division in plants, as in animals, is preceded by nuclear division, after which a cell wall is formed between the daughter protoplasts. The nucleus in the resting condition contains granular material called *chromatin*, which may be readily colored (stained) by certain dyes. Generally there are also present one or more globular bodies called *nucleoles* (Fig. 170, *A*). Chromatin is a proteid and is believed to be the essential substance of the nucleus and necessary for the life of the cell, because protoplasm will not live if deprived of nuclei. Just previous to nuclear division the chromatin becomes organized into a number of bodies called *chromosomes*, each of which splits, and the halves are distributed in two sets to the daughter nuclei. The distribution of the chromosomes is effected by an interesting apparatus called a *spindle* (Fig. 170, *B*), which consists of delicate fibers (spindle fibers) formed in the early stages of nuclear division. The two sets of daughter chromosomes (Fig. 170, *C*) collect at the poles of the spindle to organize the daughter nuclei, which then pass into the resting condition (Fig. 170, *D*), and a cell wall is formed between, that divides the original cell into two daughter cells. It is a remarkable fact that the number of chromosomes in the nucleus is fixed for different plants, — a point which we shall have occasion to consider in other connections.

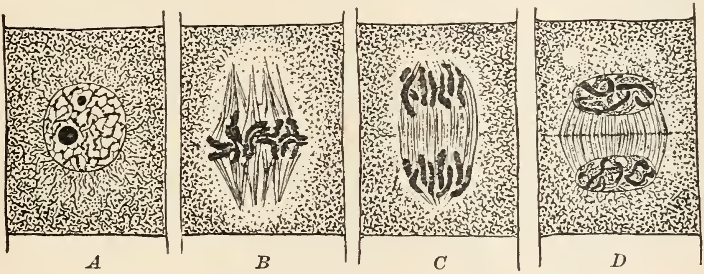

Fig. 170. Stages in nuclear and cell division from the root tip of an onion

A, resting nucleus with the chromatin in the form of a network and two nucleoles; *B*, a spindle with the divided chromosomes gathered in the middle region and about to separate into two groups of daughter chromosomes; *C*, the two sets of daughter chromosomes at the poles of the spindle; *D*, formation of the new wall between the daughter nuclei

Chromatophores reproduce themselves by simple *fission*, or splitting, very plainly illustrated in the cells of the moss leaf (Fig. 169, *C*), and are thus passed on with each cell division.

200. The cell theory of organization. The process of growth and development of a many-celled organism is through continuous cell multiplication. Development generally begins with a cell, which both in animals and in plants is called the *egg*.

The egg is a female sexual element which normally cannot develop into a new organism until a male sexual cell, called the *sperm*, has united with it. This union is called *fertilization*, and the fertilized egg is a sexually formed cell because it results from the fusion of two sexual cells, the egg and sperm. The fertilized egg is termed an *oöspore* (meaning an egg spore), when there is a resting period before its further development, or germination. A sexual cell, such as the egg or sperm, is called a *gamete*. The protoplasmic union of egg and sperm is very complete, for the two nuclei come together in the center of the egg and fuse to form a large nucleus which has, of course, about twice as much of that important nuclear substance, chromatin, as the single nucleus of either egg or sperm.

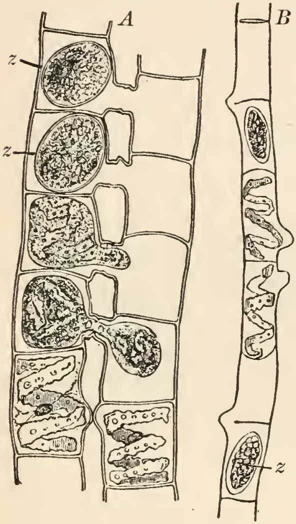

Fig. 171. The union of the gametes in *Spirogyra*

A, two filaments of *Spirogyra quinina*, side by side, showing stages in the union of the cells (gametes) to form the zygospores; *B*, another species (*S. longata*), in which the cell unions occur between adjacent gametes in the same filament. — After Schenck

Frequently there are present in plants other forms of reproductive cells called *spores*, which are not formed sexually but are simply special cells which can develop at once into new plants.

The union of gametes to give sexually formed cells is especially well illustrated in the fruiting[1] of the pond scum (*Spirogyra*). In most species the cells of filaments lying side by side put forth short processes which fuse in pairs, thus presenting a characteristic ladder-like arrangement (Fig. 171, *A*). The contents of one cell then pass over and

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[1] The terms *fruit* and *fructification* will be used in Part II in an untechnical sense to designate various forms of reproductive organs and processes.

unite with that of the other, giving a large fusion protoplast which develops a heavy protective wall and is a sexually formed spore. It is called a *zygospore* (meaning yoked spore) because the gametes are similar, like the halves of a yoke. This cell union is the same in all essentials, including the final fusion of the two nuclei, as the fertilization of the egg, except that the two sexual cells, or gametes, are not different in form as are eggs and sperms (examine illustrations of *Volvox* (Fig. 178), *Œdogonium* (Fig. 182), *Fucus* (Fig. 199), etc.). The fruiting of *Spirogyra* is a relatively simple illustration of a sexual process, for the gametes are similar and have never become differentiated into eggs and sperms.

Development proceeds through continued cell divisions, which lead to growth and a gradual specialization or setting apart of certain cells for particular kinds of work in the body. This specialization of cells results in the various forms of cell structures, or *tissues*, of the mature organism. So the life history is a succession of cell divisions, and the reproduction of the species is a return to a one-celled condition through the reproductive cells (gametes and spores). The animal and plant body dies, but the stream of life flows on through the reproductive cells. This is the outline of the cell theory of organization, which perhaps ranks next to the theory of organic evolution as one of the fundamental principles of biological science.

201. Properties peculiar to living matter. We have noted that the chemical composition and reactions of protoplasm are exceedingly complex, but nevertheless there are no reasons for supposing that they are outside of chemical and physical laws. However, protoplasm has properties which distinguish it from lifeless matter (see also Secs. 45–47).

Protoplasm has the power of growth and repair. This means that protoplasm can manufacture living substance out of the lifeless and add the same to itself. It can replace with new and fresh living matter the waste material which is used up or discarded during the life processes.

Protoplasm has the power of reproduction. Reproduction accompanies growth and depends upon cell division. Of course the surface area of a cell cannot increase in the same ratio as its bulk. The surface is the region of the cell through which some of the most important life processes of assimilation and respiration take place, and a certain amount of cell surface is necessary for a given bulk of protoplasm. Therefore the cell divides when, after a period of growth, the bulk of protoplasm becomes proportionally too great for the amount of surface area. The sum total of the surfaces of the daughter cells is materially increased by their division, while the combined bulk of their protoplasm remains the same as before.

A living being is like a machine in that it requires fuel to generate its energy or power of doing work, but the organism has the peculiar ability of making its own repairs, of increasing in size, and of detaching from itself portions which can in their turn attain the structure and efficiency of the parent. The process of life is continuous, although the material of protoplasm is constantly changing, — that is, substances are constantly going into the organism and substances are going out. It may be compared to a whirlpool in a river: the form and action of the whirlpool is constant, although the water which enters and leaves remains for only a short time in circular movement.

Protoplasm always comes from preëxisting protoplasm. This means that protoplasm, so far as we know, never springs into existence from inorganic material. It is never formed *de novo.* There have been naturalists and philosophers who believed that life might arise spontaneously under favorable conditions in suitable nutrient solutions. They cited such illustrations as the swarming microscopic life which appears in extracts or infusions of animal and vegetable matter as examples of *spontaneous generation.* These theories were overthrown chiefly by the work of Pasteur and Tyndall, who showed that life never appears in these extracts and infusions provided proper care is taken to kill all organisms that may be in them, together with all spores or other reproductive cells, and then to prevent the entrance of any more germs. An experiment in this line can be performed by heating an extract in a flask, closed by a plug of cotton, until all germs have been killed. Such a solution then will not even produce the bacterial growths that cause decomposition, for the cotton plug prevents the entrance of any dust. It is now established that all organisms at present on the earth are generated only by their like; that life only comes from life, and protoplasm from preëxisting protoplasm.

202. The distinctions between animals and plants. Plants in general are distinguished from animals by two important peculiarities.

First. The presence of chlorophyll, or equivalent pigments, enables the plant to manufacture its own food by photosynthesis in the interior of its own cells. Animals require foods already manufactured by other animals or plants, and this food is absorbed from without the cell.

Second. Plants, when growing, are generally stationary, with a firm, widely expanded, rigid structure, while animals are more rounded, compact, and yielding. These differences are determined by the fact that the protoplasts of plants are inclosed in cellulose compartments. The cell wall gives to plant structure a degree of stiffness which greatly limits or almost prevents movement, but the individual protoplasts of plants have all the characteristics of life in common with animal cells, — sensation, movement, and the powers of growth, repair, and multiplication.

203. Some organisms of doubtful position. Several groups of lowly organisms have characters which are in part plant-like and in part animal-like. We shall consider briefly only one of these groups, the flagellates.[1]

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[1] Another large group of doubtful position is the slime molds, or *Myxomycetes*, more frequently included among plants than among animals, but too special for this account. See MacBride, *The North American Slime Moulds*, 1899.

204. The flagellates.[1] The flagellates (*Flagellata*) are aquatic, motile forms, either one-celled or consisting of colonies of cells held together in a common gelatinous secretion. The individual cells are provided with one, two, or sometimes more delicate hair-like appendages called *cilia* (singular, *cilium*, meaning an eyelash), which move rapidly in the water and are organs of locomotion. Some forms have chromatophores and can therefore manufacture their own food, while others are colorless and take their food in animal fashion through a funnel-like depression into

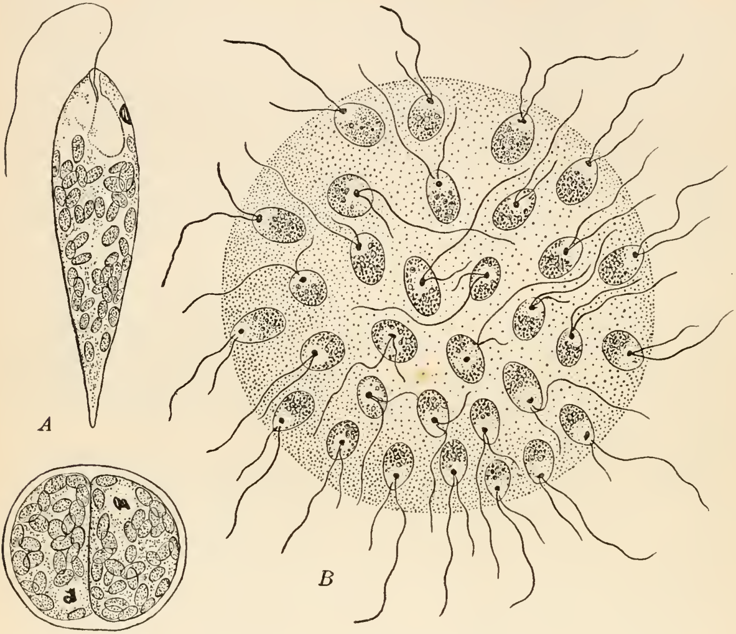

FIG. 172. Two flagellate forms

A, *Euglena*, the motile cell shown above, with its cilium and pigment spot at the forward end, the process of reproduction by simple division while in a resting condition being illustrated below; *B*, *Uroglena Americana*, a large colonial flagellate. — *B*, adapted after Moore

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[1] The best account of the flagellates will be found in Engler and Prantl, *Die Natürlichen Pflanzenfamilien.*

the interior of the cell. A bright red pigment spot, frequently found in each cell, is regarded as a structure sensitive to light, for these organisms generally move towards the source of bright illumination. The flagellates are believed to be related to the lowest green plants, the algæ, and some groups of algæ are thought to have been derived from them.

Euglena (Fig. 172, *A*) is a common flagellate found in stagnant pools. The cells are generally green, but some of the species and related forms are colorless, having adopted the habit of living exclusively on organic food substances in the drainage water which they frequent. *Euglena gracilis* becomes quite colorless when cultivated in solutions of sugar away from the light, thus suggesting the way in which colorless plants, such as the fungi, may have arisen from chlorophyll-bearing ancestors under an environment which supplied an abundance of organic food.

Uroglena (Fig. 172, *B*) is a colonial flagellate which frequently appears during the summer months in reservoirs and gives a fishy, oily taste and odor to the water, making it unfit for use. The taste and odor are caused by globules of oil that are set free by the rupture of the delicate cells when the water is carried through pipes. This is one of the organisms which can easily be destroyed by treating reservoirs with copper sulphate.[1]

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[1] See papers by Moore and Kellerman, United States Department of Agriculture, Bureau of Plant Industry, *Bulletin 64*, 1904; also *Bulletin 76*, 1905.

CHAPTER XIX

THE THALLOPHYTES

205. The thallophytes. The branch *Thallophyta* (meaning thallus plants) contains the lowest forms in the plant kingdom. A *thallus* is a simple vegetative body, without stems, leaves, or roots, in the usual sense. The groups of the thallophytes fall naturally into two series known as algæ and fungi.

The algæ. The algæ contain chlorophyll or other pigments which can do the work of photosynthesis.

The fungi. The fungi have no chlorophyll, and must therefore obtain their food either as *parasites* from the tissues of living plants or animals, called their hosts, or they may live as *saprophytes* (meaning decay plants) upon the products of decay.

The fungi are believed to have been derived from algæ which lost their color and gave up the processes of photosynthesis because they happened to be placed under conditions favorable to a life of saprophytism or parasitism. A perfect classification of the thallophytes should show the relationships of the fungi to the algæ, but these are so little understood that it seems best for the present to treat the two groups separately.

The thallus is not really the distinguishing character of the thallophytes, for some higher plants, as the liverworts, have thalloid plant bodies, and some of the algæ have a stem and leaf structure as complex as that of the mosses. The thallophytes are separated from the next higher group, the bryophytes (liverworts and mosses), by the absence of a peculiar type of life history characterized by certain complicated reproductive organs. These peculiarities cannot be understood until the liverworts and mosses have been studied, so a full definition of the thallophytes will be deferred until the end of Chapter XXIV.

CHAPTER XX

THE ALGÆ, THE LOWEST GREEN PLANTS

206. The algæ.* For the present we may think of the thallophytes as the immense assemblage of plants below the liverworts, mosses, ferns, and seed plants. In number of species and divergent evolutionary lines the group is much the largest of the four divisions of the plant kingdom (*Thallophyta*, *Bryophyta*, *Pteridophyta*, and *Spermatophyta*).

The algæ are thallophytes whose plant bodies are colored because the cells contain chromatophores. Almost all of the fresh-water forms are green, but the majority of the marine algæ, or seaweeds, are either brown or of beautiful shades of red. The green color is, of course, due to chlorophyll, while the brown and red tints are caused by other pigments. The algæ are divided into four classes as follows:

Class I.	The blue-green algæ, or *Cyanophyceæ*.
Class II.	The green algæ, or *Chlorophyceæ*.
Class III.	The brown algæ, or *Phæophyceæ*.
Class IV.	The red algæ, or *Rhodophyceæ*.

It might appear from the above that the algæ are classified by their color, but this is not true. These four groups are defined by peculiarities of cell structure, life history, and methods of reproduction which can only be understood through a study of types in the laboratory, and the summaries of these characters

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*To the Instructor: This chapter describes many more types than it would be desirable to present in a general course. The instructor should make selections according to the material available (which varies greatly in different sections of the country), and the time at the disposal of the class. A brief discussion of the best and most available types, and the reasons why they are desirable for laboratory work will be found in the laboratory manual of the authors.

must follow the accounts of the groups. However, it is an interesting fact that representative algæ of these four classes can generally be picked out at a glance by their color alone.

CLASS I. THE BLUE-GREEN ALGÆ, OR *CYANOPHYCEÆ*

207. The blue-green algæ. The simplest types of plants are found among the blue-green algæ and in that related group of the fungi called the bacteria. Some of these plants are the most primitive forms of life now present on the earth.

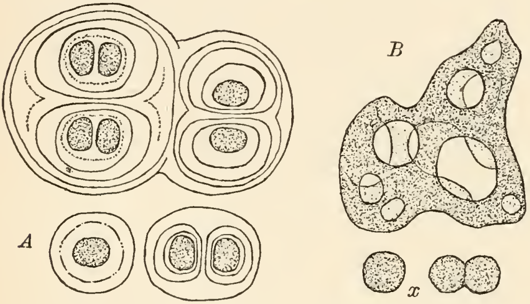

Fig. 173. One-celled blue-green algæ and their cell colonies

A, *Glœocapsa*, solitary cell and small groups held together by the thick gelatinous envelopes; *B*, *Clathrocystis æruginosa*, cell colony of many hundreds of protoplasts imbedded in a jelly-like substance; *x*, single cells illustrating division by fission

208. The one-celled blue-green algæ. These forms may develop as slimy growths on the surface of stones, woodwork, and other objects, but certain types float freely in the water in small groups, or sometimes in large cell colonies. The following types are representative.

Glœocapsa[1] (Fig. 173, *A*) consists of cells with peculiar soft walls which form concentric envelopes around the groups of protoplasts. It is evident that the wall of each protoplast persists for a long time after every cell division, so that groups of

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[1] *Chroöcoccus* is an excellent substitute for *Glœocapsa*, and is not uncommon in stagnant pools and on wet clay banks. Its cells are solitary and lack the gelatinous envelopes of *Glœocapsa*.

daughter, granddaughter, and even great-granddaughter cells may remain inclosed in the envelope of the original mother cell, which becomes very much swollen and jelly-like. The outer walls of the groups of cells finally become changed to a soft mucilage, so that the groups of *Glœocapsa* cells form at times slimy, dark green patches over damp earth, rocks, and logs. The individual protoplasts have an exceedingly simple structure, for the coloring matter is uniformly distributed through the cells and no nucleus can be seen.

Clathrocystis and *Cœlosphærium* are free, floating cell colonies, often forming greenish scums during the summer months on the surface of park ponds, reservoirs, and other small bodies of water. The colonies of *Cœlosphærium* are spherical, while those of *Clathrocystis* (Fig. 173, *B*) become irregular in shape through the development of holes, so that the structure is somewhat net-like.

209. The filamentous blue-green algæ. These frequently form felted or tufted growths or gelatinous expansions of considerable size. There are a number of complex branching types, but the following are good examples of the assemblage.

Oscillatoria is the most interesting type of the *Cyanophyceæ* if only one form can be studied. The filaments are generally made up of flattened disk-shaped cells, placed face to face within an exceedingly delicate sheath, much like a roll of coins wrapped in paper. Cell division takes place in all portions of the filament, and several stages are illustrated in Fig. 174, *A*. Growth is therefore not confined to the tip or any other special region of the plant. New filaments arise by the breaking apart of the older ones, generally at some point where one or more cells have died (Fig. 174, *A*, *d*). The end cells of filaments or fragments of filaments are always rounded, illustrating beautifully the phenomenon of cell turgor or pressure from within the protoplast upon the cell membrane. The cell structure of *Oscillatoria* is very typical of the blue-green algæ. The blue-green pigment gives color to the entire outer region of the protoplast, which may be considered a diffused chromatophore. There is no nucleus in the usual sense of the term, although the central region of the cell has a different structure from the outer and probably contains chromatin. The small granules arranged along the cross walls are believed to be food products built up by the activities of the blue-green pigment in sunlight (photosynthesis). *Oscillatoria* takes its name from the remarkable movements of the filaments, whose free ends swing back and forth describing a circle or an ellipse, while the filaments may glide slowly forward. The cause of this movement is not understood. *Oscillatoria* is found in greatest abundance in open drains, ditches, or pools, where the water is foul with decaying organic matter. There it may form thick felts on the bottom, or rise to the surface in slimy masses because of the bubbles of gas, largely oxygen, formed during the processes of photosynthesis and held within the tangle of filaments.

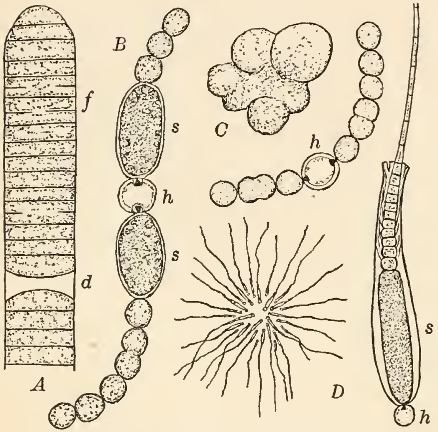

FIG. 174. Filamentous blue-green algæ

A, *Oscillatoria*; *d*, dead cell, indicating a point where the filament might break apart; *f*, stages of cell fission; *B*, *Anabæna*; *h*, heterocyst; *s*, resting cells; *C*, *Nostoc*, habit sketch of a colony and the details of a single filament; *h*, heterocyst; *D*, *Glœotrichia*, portion of a colony and the base of a single filament in detail; *h*, heterocyst; *s*, resting cell

Anabæna and *Nostoc* are closely related genera. The filaments are chains of round or elliptical cells. Besides the blue-green vegetative cells there are present at intervals curious cells termed *heterocysts* (meaning other cells), which are generally larger than the vegetative cells, lighter in color, and often empty of protoplasm. Their function is not clearly understood. The filaments may break apart on either side of the heterocyst, setting free chains of cells which grow into new filaments. Certain vegetative cells in *Anabæna* increase greatly in size and become densely filled with protoplasm and food material and surrounded by a thick protective wall (Fig. 174, *B*, *s*). Such cells are called *resting cells*, or spores, and they are able to live through seasons of drought or a winter's cold and with the return of favorable conditions to germinate and form new filaments. The filaments of *Anabæna* are held in a soft slime, but those of *Nostoc* are surrounded by a stiff jelly, so that the mass of much-coiled chains of cells has a firm boundary. Consequently, *Nostoc* colonies (Fig. 174, *C*) may have a spherical form and become as large as marbles. The slimy or jelly-like substance of *Anabæna* and *Nostoc* is a modification of the delicate sheath around the filaments and corresponds to the envelopes about the cells of *Glœocapsa*.

Glœotrichia (Fig. 174, *D*) sometimes develops in such quantities in ponds and lakes during the summer as to form a brilliant green scum on the surface of the water. The filaments have a radiate arrangement in a soft, gelatinous substance and end in long hairs, and a very large resting cell may be formed at the base of each filament adjacent to the terminal heterocyst.

210. Life habits of the blue-green algæ. The *Cyanophyceæ* have some peculiar life habits of ecological interest. They are generally found in warmish waters, both fresh and salt, and many of the forms prefer those which are foul with decaying organic matter. Thus open drains and reeking pools of stagnant water present luxuriant growths of these algæ. It is probable that the plants actually use for food certain of the organic substances in such waters. Some of the most conspicuous green scums on ponds and small lakes are composed of certain of these algæ (*Cœlosphærium*, *Clathrocystis*, *Anabæna*, and *Glœotrichia*, etc.). Such scums may be called water blooms, after the German term *Wasserblüthe*. The coloration of the Red Sea is due to an extensive water bloom caused by a filamentous blue-green alga (*Trichodesmium*) which at times fills the water, and whose color, a reddish brown, gives then a peculiar tint to the sea.

Some forms (*Anabæna, Clathrocystis,* and certain species of *Oscillatoria*) are frequently responsible for the fouling of water supplies which take on what is called the "pigpen odor," and are otherwise unfit for public use. All of these blue-green algæ, together with the flagellate *Uroglena,* can be killed by treating the reservoir or other body of water with copper sulphate (see Sec. 204), a perfectly safe and inexpensive remedy for contaminated water supplies.

Perhaps the most remarkable display of the blue-green algæ is in the waters of certain hot springs, as in Yellowstone National Park. It is doubtful whether any algæ except the *Cyanophyceæ* can live in water warmer than 100° F. (40° C.), but some of the blue-green algæ grow luxuriantly in hot springs at 137°–145° F. (58°–63° C.). It is probable that their simple cell structure makes possible a greater power of resistance to these extraordinary life conditions.

211. Summary of the blue-green algæ. The *Cyanophyceæ* are distinguished from other groups of algæ by the simplicity of their cell structure, the absence of sexual reproduction, and the presence of a blue-green pigment uniformly diffused through the outer region of the cells. The method of growth by rapid divisions or splitting of the cells throughout the entire plant body is a very characteristic feature of the group, and the blue-green algæ are sometimes called the "fission algæ" (*Schizophyceæ*).

The blue-green algæ agree with the bacteria, or "fission fungi" (*Schizomycetes*), in their simplicity of cell structure and methods of reproduction, but the bacteria are of course generally without pigment. It is quite clear that the *Cyanophyceæ* and the *Schizomycetes* are closely related, and some authors place them together in a separate division of the plant kingdom below the *Thallophyta*, named the *Schizophyta,* or "fission plants."

CLASS II. THE GREEN ALGÆ, OR *CHLOROPHYCEÆ*

212. The green algæ. The green algæ comprise a large and varied assemblage of groups, many of which are widely different from one another. Some forms of the *Chlorophyceæ* are believed to stand rather close to what was the main line of ascent from the algæ to the liverworts and mosses. Consequently the class has an important place in an account of the evolution of the plant kingdom. The green algæ illustrate better than any other group the origin and evolution of sexual processes in plants. Since the more familiar algal growths of fresh water are green algæ, a more extended treatment of the *Chlorophyceæ* will be given than of the less familiar groups of the *Cyanophyceæ*, *Phæophyceæ*, and *Rhodophyceæ*, and the following six orders will be considered together with a "Summary of the Green Algæ."

Order 1. The one-celled green algæ, or *Protococcales*.
Order 2. The confervas, or *Confervales*.
Order 3. The pond scums and desmids, or *Conjugales*.
Order 4. The diatoms, or *Diatomales*.
Order 5. The siphon algæ, or *Siphonales*.
Order 6. The stoneworts, or *Charales*.

ORDER 1. THE ONE-CELLED GREEN ALGÆ, OR *PROTOCOCCALES*

213. The one-celled green algæ. This order contains almost all of the one-celled green algæ excepting the large but very special groups of the desmids and diatoms. We can only describe briefly five types.

214. Pleurococcus. *Pleurococcus* (family *Pleurococcaceæ*) forms the green coating or stain that is very common on the north sides of tree trunks, fences, and stone walls. The cells (Fig. 175) may be solitary, but they usually remain associated in small groups for some time after the cell divisions. The protoplast contains generally a single chromatophore of irregular shape which, as a rule, fills the greater part of the cell. The chromatophore is, however, variable in size and may or may not have a pyrenoid (Sec. 196). The nucleus can sometimes be seen in the center of the cell. The cells are exceedingly resistant to cold and drought, but under very severe conditions they protect themselves by forming a heavy cell wall, thus becoming resting cells. Sometimes the contents of a cell break up into several daughter protoplasts, but as a rule the only method of reproduction is by simple cell division. Other forms of one-celled algæ, with more complicated methods of reproduction (by zoöspores and gametes), are frequently found associated with *Pleurococcus*, but should be carefully distinguished from this simple alga.

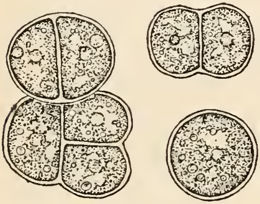

FIG. 175. *Pleurococcus vulgaris*, a one-celled green alga

Several cells illustrating the method of cell division and their association in small groups

Pleurococcus may seem almost as simple as the one-celled blue-green alga *Glœocapsa*, but its cell structure with a chromatophore and well-defined nucleus is far in advance of the *Cyanophyceæ*.

215. Sphærella and Volvox.* These forms are representatives of one of the most interesting families of the green algæ, the *Volvox* family[1] (*Volvocaceæ*). The lowest members are one-celled and resemble the flagellates (Sec. 204), but the higher forms are cell colonies of remarkable structure and life histories. The vegetative cells are motile, being always provided with two

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* TO THE INSTRUCTOR: It is rather difficult to obtain material of the *Volvox* family, and it cannot be depended upon for type study. Therefore laboratory work on the reproductive processes in the algæ can much better be arranged with such types as *Ulothrix*, or *Ulva*, or some form of the *Chætophoraceæ*, or *Cladophora*, *Œdogonium*, or *Vaucheria* and *Fucus*. But the *Volvocaceæ* and *Flagellata* are so important to a conception of certain primitive conditions of algal life that they should be discussed in any extended general course. The fact that zoölogists have found *Volvox* and its relatives of interest should not deter botanists from making use of their own.

[1] For a detailed account of the *Volvocaceæ* see Goebel, *Outlines of Classification and Special Morphology of Plants*, and Engler and Prantl, *Die Natürlichen Pflanzenfamilien.*

hair-like cilia, whose incessant whipping of the water carries the organism along. There is also a red pigment spot at the ciliated end of the cell (Fig. 176, *A*, *p*). This free-swimming, ciliated cell is of a type strikingly different from *Pleurococcus*, but it is believed to represent very nearly the ancestral condition of many groups of algæ.

Sphærella lacustris (*Hæmatococcus pluvialis*) is found freely swimming in rock pools and sometimes in troughs and basins, and is frequently so abundant as to color the water a bright green. The organism multiplies very rapidly, for the larger individuals (Fig. 176, *A*) form 2–16 daughter cells (Fig. 176, *B*), which escape from the mother-cell membrane, swim away, and after a period of growth form in their turn a new set of daughter cells. The free-swimming cells come to rest at times, becoming thick-walled resting cells, which are colored red by a peculiar pigment. These resting cells carry the plant over

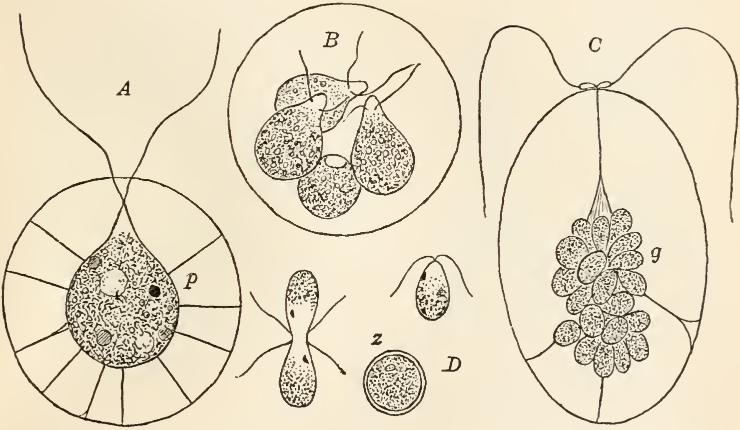

Fig. 176. *Sphærella*

A, *B*, *Sphærella lacustris:* a single cell in detail and a group of daughter protoplasts within the parent cell. *C*, *D*, *Sphærella Bütschlii:* numerous small sexual elements or gametes are shown in the parent cell *C*, and *D* illustrates their fusion in pairs to give the sexually formed cell or zygospore *z*.—*B*, after Schenck; *C*, *D*, after Blochmann unfavorable seasons and are sometimes developed so numerously as to cover the bottom of pools and rock hollows with a red deposit. The phenomenon called "red snow" is due to deposits of the resting cells of *Sphærella nivalis* on fields of snow and ice.

Some species of *Sphærella* (Fig. 176, *C*) develop a much greater number of daughter elements, 32 to 64, which are much smaller than those just described, but have the same structure. These smaller cells swim about freely for a short time, and then come together in pairs and completely fuse with one another, beginning at the ciliated ends (Fig. 176, *D*). A cell fusion of this character is a sexual act (Sec. 200) and the cells which unite are *gametes*. The sexually formed fusion cell or *zygospore* of *Sphærella* soon settles down on some surface and, losing its four cilia, remains quiet for several days or weeks, finally developing within itself several motile cells of the usual type.

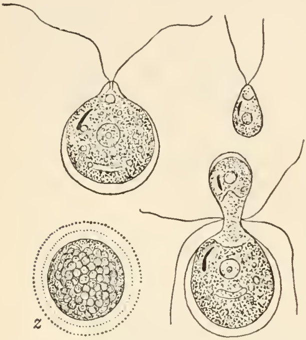

Fig. 177. *Chlamydomonas Braunii*

Chlamydomonas is not uncommon in the same sort of situations as *Sphærella*. It may be distinguished from the latter by the absence of a thick gelatinous envelope around the cells. Some of the forms show important advances over *Sphærella* in their sexual processes, for the gametes may be of two sizes, large female and small male cells, as shown above. *z*, the zygospore. — After Goroschankin

Volvox (Fig. 178, *A*) is a colonial form consisting of many hundreds of cells (sometimes more than twenty thousand) imbedded in a gelatinous substance in the form of a sphere, with the pairs of cilia pointing outwards. These remarkable organisms, as large as pin heads, roll slowly through the water of quiet pools and ponds, sometimes gathering in great numbers in open sunlit portions, free from water weeds and algal growths. Daughter colonies (Fig. 178, *A*, *d*) are formed from certain cells which after a period of growth develop a large number of motile cells like the parent. These small cells become arranged to form a daughter colony which swims around in the interior of the mother colony. Sometimes several of the daughter colonies may be developed, and they finally escape by the rupture of the parent structure. The sexual cells, or gametes, are of two sorts: (1) large female cells, which are called *eggs* because they are without cilia and consequently never motile, and (2) small male cells, or *sperms*, of peculiar form, with two cilia, and consequently very actively motile. The eggs

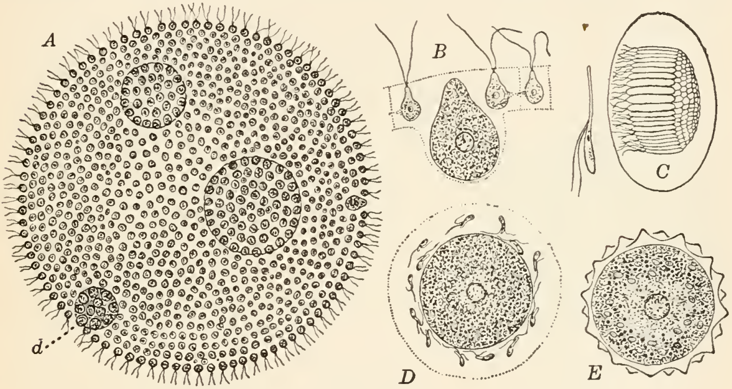

Fig. 178. *Volvox globator*, a colonial form of the *Volvocaceæ*

A, mature colony, with four daughter colonies developing in its interior; *B*, section of the edge of the colony, showing three vegetative cells and a developing egg; *C*, a packet of sperms within the parent cell and a single sperm very much magnified at the side; *D*, an egg surrounded by a swarm of sperms; *E*, an oöspore with heavy protective wall. — *C*, after Cohn.

(Fig.178, *B*, *D*), formed by the enlargement of vegetative cells, escape into the interior of the colony as naked spherical protoplasts. The sperms (Fig. 178, *C*) are developed in great numbers within enlarged vegetative cells. They are also set free within the parent colony and gather about the eggs in swarms (Fig. 178, *D*). Finally, a single sperm fuses with each egg, which is then said to be *fertilized*. The fertilized egg immediately forms a cell wall about itself and passes through a period of rest as an *oöspore* (Sec. 200).

Volvox thus presents a great advance over *Sphærella, Chlamydomonas,* and other one-celled members of the *Volvocaceæ,* in the highly developed sexual process as well as in the complex cell colony. There is, however, a series of genera (*Gonium, Pandorina, Eudorina, Pleodorina,* etc.) in the family, illustrating intermediate conditions between these extreme forms, which makes it clear that *Volvox* stands at the head of a remarkable line of development in the algæ. It may be considered the climax type of a side line of evolution,—that is, a branch which departs widely from the main line of ascent.

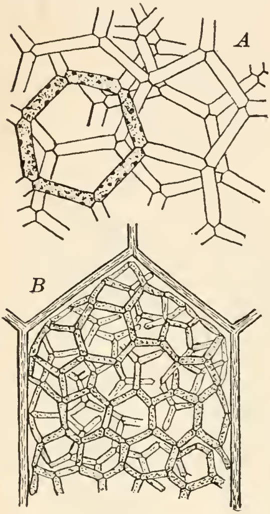

Fig. 179. The water net (*Hydrodictyon*)

This is a remarkable form of the *Protococcales,* whose cells form the meshes of a net-like cell colony, *A.* New nets are formed in the interior of large cells, *B,* which develop an immense number of zoöspores that never escape from the mother cell, but join with one another to form daughter nets, which are set free by the breaking down of the mother-cell wall

ORDER 2. THE CONFERVAS, OR *CONFERVALES*

216. The confervas. The *Confervales* comprise many very common filamentous algæ and also such membranous forms as the sea lettuce. The algæ which seem to be nearest to the main line of ascent to the liverworts and mosses are found in this group. Some of the types illustrate especially well the principal forms of sexual reproduction in the algæ and various types of life histories.

217. Ulothrix. This confervoid alga (family *Ulothricaceæ*) is abundant on stones and rocks along the shores of the great lakes, in quieter waters at the seaside, and frequently grows in stone fountains or on stonework around park ponds. The filaments are unbranched, and each consists of a row of similar cells. Each cell contains a single chromatophore with pyrenoids, which has the form of a wide band, or girdle, just under the cell wall, and generally surrounds the nucleus in the middle region of the cell (Fig. 180, *A*, *B*). The filaments are attached at one end (Fig. 180, *A*), and the growth by cell division takes place throughout the entire length and is not confined to the tip as in some algæ. The cells in the upper portions of older filaments (Fig. 180, *B*) develop a type of reproductive cell very common among the algæ, called the *zoöspore* (meaning animal spore) because of its animal-like habit of swimming about.

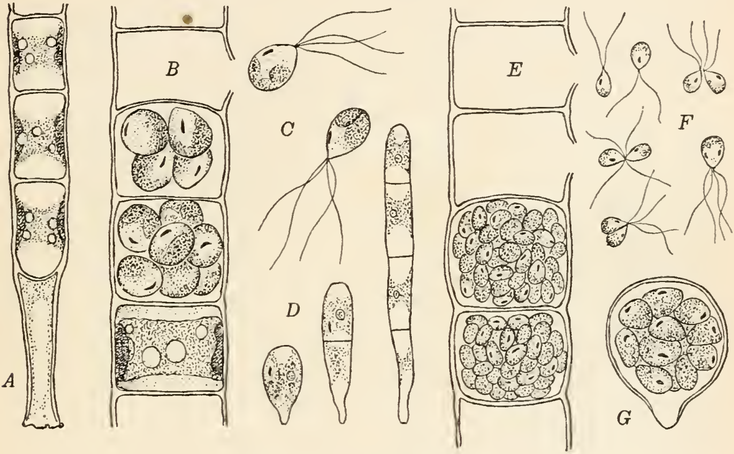

Fig. 180. *Ulothrix zonata*

A, base of filament, showing its attachment and cells containing band-shaped chromatophores with pyrenoids; *B*, portion of a filament about fifty cells above the base, showing a vegetative cell below and two cells which have formed 4 and 8 zoöspores respectively; *C*, the zoöspores, each with a pigment spot and four cilia; *D*, stages in the germination of the zoöspore; *E*, portion of a filament illustrating the formation of gametes, 64 in each cell; *F*, the gametes, showing pigment spot and two cilia, and stages in their fusion to form a four-ciliate zygospore with two pigment spots; *G*, germination of the zygospore, which develops a number of zoöspores. — *G*, after Dodel

Zoöspores are naked ciliated protoplasts formed within parent cells called *sporangia*. They swim rapidly through the water, and each generally contains a red pigment spot. Zoöspores are attracted by light and collect at the illuminated side of a vessel, forming a green cloud in the water. Because of these habits, and their rapid darting to and fro in the water, they are often called *swarm spores.*

The zoöspores of *Ulothrix* are developed most numerously at night and are set free from the parent filaments chiefly during the morning hours. Sometimes the entire protoplast slips out as a single large zoöspore, but more often 2, 4, or 8 zoöspores are formed in each parent cell (Fig. 180, *B*). They are roundish or pear-shaped (Fig. 180, *C*), with four cilia at the pointed end, and each contains a red pigment spot, chromatophore, and nucleus. The zoöspores thus resemble the organisms called flagellates (Sec. 204), and like them swim freely around in the water by the lashing movements of their cilia. But the zoöspores have a relatively short free-swimming period, for after perhaps an hour or more they attach themselves by the ciliated ends to various objects and grow into new *Ulothrix* filaments (Fig. 180, *D*).

At times a much greater number of zoöspores may be developed in the parent cells, — perhaps 32 or 64, or even more than a hundred (Fig. 180, *E*). These have generally only two cilia and are much smaller than the four-ciliate zoöspores, but otherwise have the same structure. They swim very actively for a short time, and then come together in pairs in the water and fuse with one another (Fig. 180, *F*). This cell union is a sexual process (see Sec. 200), and the small two-ciliate zoöspores are therefore sexual elements and are called *gametes.* The result of this fusion is a sexually formed cell called a *zygospore* (meaning a yoked spore), because the two gametes are similar, like the halves of a yoke, and not different in form, as the sperm and egg (see Fig. 178, *Volvox*). This simple type of sexual reproduction is termed *isogamy,* because the gametes have the same form, or morphology. The zygospore, of course, corresponds to the fertilized egg, or oöspore, characteristic of higher plants.

The zygospore of *Ulothrix* swims about for a short time with its four cilia, and may only be distinguished from the large four-ciliate asexual zoöspores by its two pigment spots. It finally comes to rest and remains quiet for many weeks or several months, but slowly increases in size. Finally, the zygospore develops several zoöspores (Fig. 180, *G*), which escape from the cell, swim off, and develop new *Ulothrix* plants.

218. The sea lettuces. The sea lettuces include *Ulva* and its relatives (family *Ulvaceæ*), and are very common along the seacoast, forming green fringes on the rocks and wharves near low water-mark. The thallus is a thin green membrane (Fig. 181, *A*) instead of a filament as in *Ulothrix*. Zoöspores and gametes (Fig. 181, *B*, *C*) are developed in the cells along the edge of the membranes. Their structure, methods of formation, and habits are essentially the same as in *Ulothrix*, and the sea lettuces are equally good for the study of these points, and they are sometimes more available than *Ulothrix* for those living at or near the seacoast.

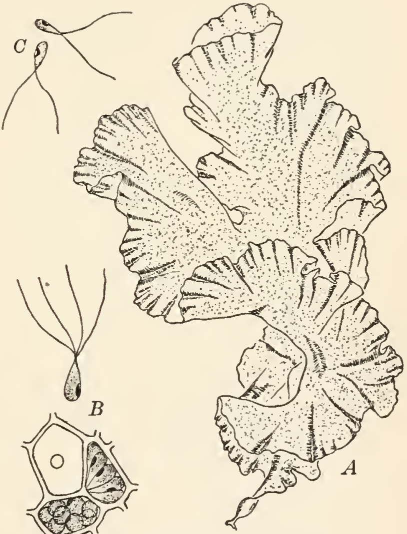

FIG. 181. The sea lettuce (*Ulva*)

A, habit sketch; *B*, cells forming four-ciliate zoöspores; *C*, two-ciliate gametes.—Adapted after Thuret

219. The origin of sex in plants. *Ulothrix*, *Ulva*, and some other types show clearly that the simplest forms of gametes in plants are closely related to zoöspores, for they are developed in the same way and have a similar structure. Indeed, the gametes of these lower plants frequently germinate directly like zoöspores, thus showing that the sexual habit of fusing with one another is not firmly fixed. However, the plants that develop from such gametes are generally smaller and weaker than those which come from the usual zoöspores. For these reasons it seems evident that the gametes of plants arose from zoöspores, or motile cells similar to zoöspores, which, adopting the habits of fusing in pairs, became sexual cells. Such types as *Ulothrix* and *Ulva* have an especial interest because they illustrate the general conditions which must have been present with the origin of sex in any group of plants.

220. Œdogonium. *Œdogonium* (family *Œdogoniaceæ*) is one of the best illustrations in the green algæ of the higher sexual condition where the gametes become differentiated and specialized as eggs and sperms.

The species are unbranched, filamentous, fresh-water forms, attached by a disk-like development from the lowest cell (Fig. 182, *A*) called a *holdfast.* The cells have large chromatophores of irregular form, containing pyrenoids. There are sets of curious lines called *caps* across the ends of many of the cells (Fig. 182, *B*, *c*), — structures peculiar to this family, — which result from a method of cell division too complicated to be described here.[1] Zoöspores are developed singly in the cells, and are large protoplasts with a circle of cilia at a colorless end (Fig. 182, *D*). After swimming about for a short time the zoöspores settle down on the ciliated end, develop the holdfasts, and grow at once into new filaments.

The sexual cells, or gametes, of *Œdogonium* are *eggs* and *sperms.* The eggs are developed singly in enlarged cells, which are the female sexual organs (Fig. 182, *B*) and are called *oögonia* (singular, *oögonium*). The entire protoplast of the oögonium becomes the egg (Fig. 182, *B*, *e*), which remains within the oögonium as a naked, motionless cell, without cilia, and is richly supplied with chromatophores and food material. The sperms are developed in pairs in short, disk-shaped cells, which are found in small groups, forming the male sexual organ, or

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[1] See Goebel, *Outlines of Classification and Special Morphology of Plants*, p. 44.

antheridium (Fig. 182, *B*, *a*). The sperms, frequently called *antherozoids* by botanists, are small, almost colorless protoplasts, with a circle of cilia at one end (Fig. 182, *C*) like the zoöspore. They are in sharp contrast to the eggs, being actively motile, ciliated, and with very much reduced chromatophore and food contents.

A cleft, or pore (Fig. 182, *B*, *e*), is formed in the oögonium so that the sperms may enter, and one of them, fusing with the egg, *fertilizes* it. The egg after fertilization develops a heavy wall (Fig. 182, *B*, *o*) and becomes an *oöspore* (meaning an egg spore). The oöspores, thus protected, can live through drought or winter's cold and so survive seasons of the year impossible for vegetative growth. On the return of favorable conditions they germinate, each oöspore

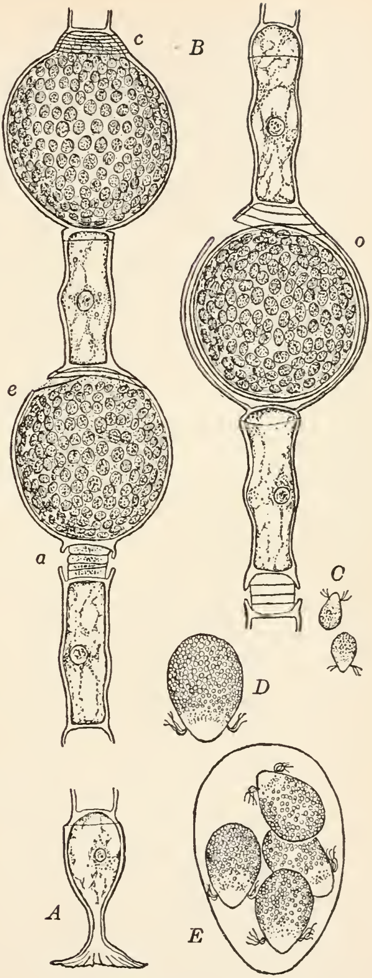

Fig. 182. *Œdogonium nodulosum*

A, base of filament showing holdfast; *B*, filaments with oögonia and antheridia; *e*, an egg ready for fertilization, showing the cleft for the entrance of the sperm; *o*, the thick-walled oöspore; *a*, antheridium, composed of four cells; *c*, caps; *C*, sperms, showing crown of cilia; *D*, zoöspore; *E*, germination of the oöspore, producing four zoöspores. — *C*, *D*, *E*, after Juranyi giving rise to four large zoöspores (Fig. 182, *E*), which develop at once into *Œdogonium* plants.

Both eggs and sperms are believed to have been derived from simpler ancestral types of ciliated gametes, similar in structure to one another and to the zoöspore. These ancestral sexual conditions must have been those of isogamy, somewhat as is at present illustrated in *Ulothrix*. The originally similar ciliated gametes varied in size. The smaller reduced their chromatophore and food contents because they were formed in large numbers but retained their cilia and thus became the small active sperms. The larger gametes accumulated rich supplies of food, became sluggish, finally lost their cilia and swimming habits, and at last were retained within and protected by the oögonia, thus becoming large nonmotile eggs.

It is clear that the plant gains very much by differentiating and specializing its gametes as eggs and sperms, for the eggs are protected and richly supplied with protoplasm and food, while the sperms are developed very numerously and are well adapted to swim actively about in the water, where they are attracted to the eggs by substances secreted by its protoplasm. The higher sexual condition, as in *Œdogonium*, where the gametes are eggs and sperms, is called *heterogamy* because the gametes are dissimilar, in contrast to *isogamy* (see account of *Ulothrix*, Sec. 217).

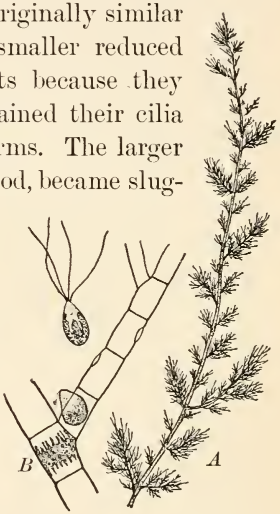

Fig. 183. *Draparnaldia*, one of the *Chætophoraceæ*

A, habit sketch; *B*, side branch, discharging large four-ciliate zoöspores formed singly in the cells

221. The Chætophoraceæ.* The members of this family, including such common genera as *Stigeoclonium*, *Draparnaldia*

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* To the Instructor: It does not seem to be generally known that forms of the *Chætophoraceæ* are almost equally good types for the study of zoöspores as *Ulothrix* and may be readily substituted for that form. *Stigeoclonium*

(Fig. 183), and *Chætophora*, are more complex than *Ulothrix*, for they consist of branching filaments of peculiar forms. However, the cell structure, life histories, methods of reproduction, and low sexual conditions (isogamy) of these types all show relationships to the *Ulothricaceæ*. They are of especial interest as leading up from the level of *Ulothrix* to the highest form of the *Confervales*, the genus *Coleochæte*.

222. Coleochæte. *Coleochæte* (family *Coleochætaceæ*) contains a number of species which live in fresh water, attached to the stems and leaves of water weeds, and they frequently appear on the sides of aquaria. Some of the forms are circular flat plates or cushions of cells that really consist of systems of filaments radiating out from a center. Large, two-ciliate zoöspores are formed singly in the cells. The female organ, oögonium, is a large, flask-shaped cell with a long neck (Fig. 185 *A*, *o*). Its protoplasm forms a single spherical egg which nearly fills the lower swollen portion of the oögonium, and the neck finally opens above to allow the entrance of the sperms. The male organs, antheridia (Fig. 185, *A*, *a*), are small cells, generally in groups, each of which develops a two-ciliate sperm.

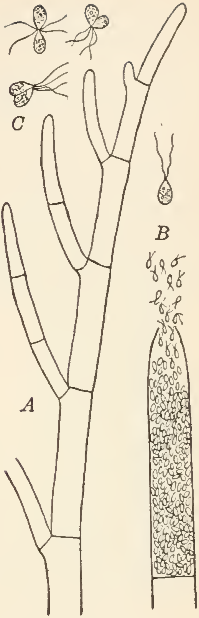

FIG. 184. *Cladophora*

This large, much-branched, filamentous alga, *A*, has many species common in both fresh and salt water. Zoöspores, *B*, are formed generally in terminal sporangia, and there are gametes which fuse in pairs, *C*, as in *Ulothrix*. The older cells contain large numbers of nuclei, and this form, with certain relatives (family *Cladophoraceæ*), occupy a position somewhat intermediate between the *Confervales* and *Siphonales*

and *Draparnaldia* are common on stones in clear brooks and in springs. *Cladophora* (Fig. 184) is also a good type for laboratory study and very common.

The fertilized egg becomes an oöspore within the oögonium and is further protected by a cellular envelope (Fig. 185, *B*) developed from short filaments which grow up around the structure (Fig. 185, *A*, *f*), making a conspicuous fructification. The oöspore germinates the following spring, forming within itself a small group of cells (Fig. 185, *C*), each of which gives rise to a zoöspore. The decay and rupturing of the fructification allows the zoöspores to escape and start new *Coleochæte* plants at the beginning of each season. The fructification of *Coleochæte* serves to multiply the number of zoöspores produced by the oöspore, which is clearly an advantage.

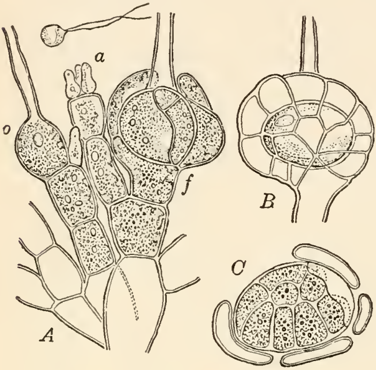

FIG. 185. *Coleochæte pulvinata*

A, filaments with an oögonium *o*, antheridium *a*, and a sperm above; *f*, fertilized egg in its oögonium becoming surrounded by short filaments from the cell below; *B*, oöspore completely inclosed in a cellular envelope derived from filaments such as are shown in *A*, *f*; *C*, germination of oöspore, each cell in the interior develops a zoöspore. — After Pringsheim

Coleochæte stands at the head of one of the best-defined lines of evolution in the algæ, a line which starts at the lowly level of the *Ulothricaceæ* and runs upwards through the *Chætophoraceæ*. Authors have generally regarded these forms as leading almost directly to the bryophytes, with *Coleochæte* just a little below the liverworts; but, as we shall see later, there are serious difficulties in the way of this view.[1] Nevertheless, these forms are perhaps nearer than any other living algæ to the theoretical main line of ascent.

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[1] The fructification of *Coleochæte* has been regarded as similar to the so-called fruit or sporophyte of the liverworts, but, as explained in Sec. 336, there is strong evidence against this interpretation. The one-celled sexual organs of *Coleochæte* are also very different from the many-celled sexual organs of the bryophytes, and this is also evidence against the existence of a close relationship between the groups (see Sec. 299).

ORDER 3. THE POND SCUMS AND DESMIDS, OR *CONJUGALES*

223. The pond scums and desmids. The pond scums and desmids (order *Conjugales*) are remarkable for the beauty and symmetry of their cell structure, and especially for their large and complicated chromatophores. There are no motile stages in their life histories, and the sexual processes consist in the union or conjugation of *similar nonmotile* gametes (isogamy). These characters distinguish the group sharply from all other algæ, but make the relationships of the forms very uncertain. These plants live only in fresh water and seek the sunshine, being abundant in clear, shallow pools. The desmids live chiefly along the margin and on the bottom, while the pond scums frequently form growths upon the surface of the water, which appear frothy because of the bubbles of gas (largely oxygen) held among the filaments. The filaments are very slippery to the touch on account of a slimy excretion from the cells.

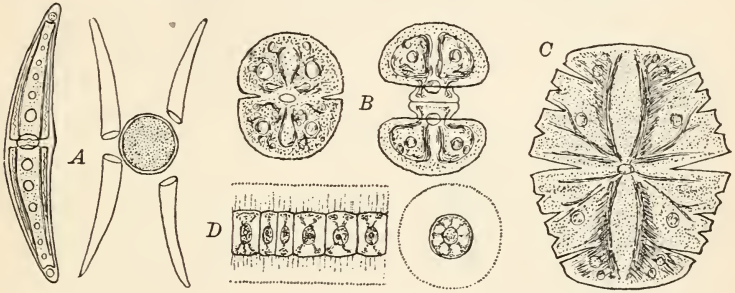

FIG. 186. Desmids

A, *Closterium*, a vegetative cell at the left and a zygospore at the right between the halves of two empty cells whose contents have fused; *B*, *Cosmarium;* the desmid at the right has just divided and is forming two new parts between the old halves of the parent cell. *C*, *Micrasterias*, a very elaborate form in its outline and markings; *D*, *Hyalotheca*, a common filamentous desmid; the appearance of the cells in face view is shown at the right

224. The desmids. There are about one thousand species in this large group whose forms are generally one-celled, although some desmids are filamentous (Fig. 186, *D*). Each cell has two parts, which duplicate one another even in the details of protoplasmic structure, and the nucleus lies in the middle region, with the chromatophores arranged symmetrically in the halves. The desmids multiply rapidly by cell division, each daughter cell taking one half of the old cell wall and adding to it a reproduction of the other half (Fig. 186, *B*). The gametes are naked protoplasts, which escape by the breaking apart of the halves of the cells and fuse in pairs, forming thick-walled zygospores (Fig. 186, *A*). In some common forms (*Closterium* and *Cosmarium*) the zygospore on germinating produces two desmids.

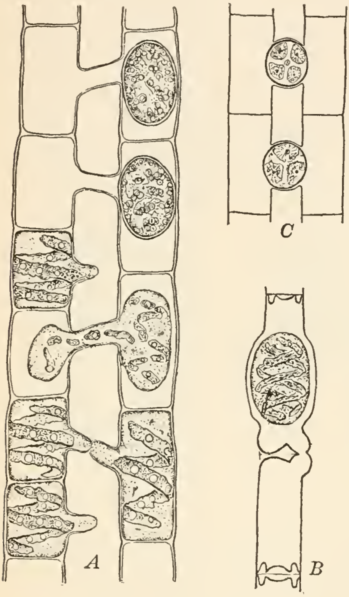

Fig. 187. Pond scums

A, *Spirogyra*, illustrating stages in the conjugation between cells of different filaments, two zygospores shown above; since the cells in the filament on the left are shorter than those on the right, some of them must be left out in the pairing of the gametes. *B*, the conjugation between adjacent cells of the same filament in *Spirogyra quadrata*; *C*, *Zygnema* (*Zygogonium*) *pectinatum*, showing zygospores formed in the conjugating tubes between two filaments

225. The pond scums. Some of the commonest and most beautiful of filamentous green algæ, such as *Spirogyra* and *Zygnema*, belong here. The complex chromatophores with their sharply differentiated pyrenoids give an especial interest to the cells and help to distinguish the genera. Thus the chromatophores of *Spirogyra* are spiral bands (Figs. 168, 187); *Zygnema* has two star-shaped chromatophores, and *Mougeotia* has a broad, thin band in the center of the cell. The method of sexual reproduction is very characteristic, but exceptional among the algæ. Generally the cells of different filaments unite or conjugate with one another by the fusion of processes, one put out from each gamete (Fig. 187, *A*). The gamete protoplast of one of the cells in the pair then passes over into the other, or in certain forms the two protoplasts unite more or less midway between the two cells (Fig. 187, *C*). In some species, however, there is a conjugation between adjacent cells of the same filament (Fig. 187, *B*), the contents of one cell entering the other. The fusion of the two gamete protoplasts results in a zygospore, which develops a heavy wall about itself as in the desmids and, as a resting spore, carries the plant over unfavorable seasons. On germination each zygospore puts forth a filament, which grows by repeated cell divisions all along its length.

ORDER 4. THE DIATOMS, OR *DIATOMALES*

226. The diatoms. The diatoms (order *Diatomales*) comprise a remarkable group of one-celled plants, containing several thousand species, everywhere present in both fresh and salt water. They compose the greater part of the floating microscopic life, called the *plankton*, of the ocean and lakes, and are the most important source of food for some of the smaller animal forms, and through them for the fish life. The cell walls are filled with the mineral silica and consist of two parts, called *valves*, which fit together something like the halves of a pill box (Fig. 188, *A*). Diatom cells have a great variety of forms, elliptical and circular, wedge-shaped and triangular, cylindrical and rhomboidal (see Fig. 188). The cells are solitary in many forms, but in others are arranged in filaments, or borne at the ends of gelatinous stalks, or held in filamentous sheaths or jelly-like masses. Many of the diatoms, and especially the boat-shaped forms, glide to and fro in the water. The cells contain chromatophores which are generally colored brown (although certain species are green), but in spite of this color the most natural position of the diatoms seems to be among the green algæ, with possible distant relationships to the desmids.

The diatoms resemble the desmids in the similar halves of the cell and in the development of a peculiar type of spore called an *auxospore,* which probably corresponds to a zygospore. Some auxospores are formed by the fusion of two gamete protoplasts which leave the diatom shells at one side (Fig. 188, *B*), and these are true zygospores very similar to those of the desmids (Fig. 186, *A*). Other auxospores are developed without protoplasmic fusions and are probably examples of sexual degeneration; that is, cells which were originally gametes now develop directly into auxospores. The auxospores are resting spores and appear to be formed after long periods of vegetative cell divisions to stimulate or rejuvenate the protoplasm for further activities.

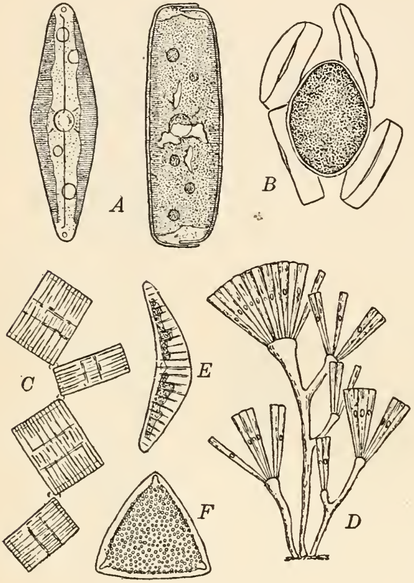

Fig. 188. Diatoms

A, *Navicula*, the boat diatom, the side view at the right showing the two overlapping shells or valves; *B*, *Acnanthes*, an auxospore with the four empty shells of the two diatoms whose contents united to produce this sexually formed spore similar to the zygospore of the desmids (see *Closterium* (Fig. 186, *A*); *C*, *Tabellaria*, groups of cells united with one another to form a zigzag filament; *D*, *Licmophora*, groups of cells borne on gelatinous stalks; *E*, *Epithemia*; *F*, *Triceratium*. —*B*, after West

The shells of diatoms, being composed of silica, resist solution in water and are constantly being deposited at the bottom of seas, lakes, ponds, and marshes, sometimes in such quantities as to form so-called siliceous or diatomaceous earths. There are some geological deposits (Tertiary) of diatomaceous earth many feet in thickness, as that at Richmond, Virginia. Some of these earths have so large a proportion of hard diatom shells as to be valuable as polishing powders, and they are also used as the absorbent of nitroglycerin in the manufacture of dynamite.

Order 5. The Siphon Algæ, or *Siphonales*

227. The siphon algæ. The siphon algæ (order *Siphonales*) differ from all other groups of algæ in the striking peculiarity that the protoplasm, with thousands of nuclei, is not separated into compartments or cells, but is all contained within a common filament or other cell cavity. Such a many-nucleate structure is called a *cœnocyte* (meaning a vessel in common). The siphon algæ are chiefly marine, and many large and complicated forms are found in the warmer seas (*Caulerpa*, *Udotea*, etc.). Some of these are heavily incrusted with lime (*Acetabularia*, *Penicillus*, *Halimeda*, etc.). Two-ciliate zoöspores and gametes are developed by certain types in cells cut off from the ends of the filaments. The gametes fuse in pairs on their escape into the water, forming zygospores. All of the siphon algæ are isogamous, when sexual at all, except the green felt, *Vaucheria*, which stands quite alone as the only heterogamous type in the group.

228. Vaucheria. *Vaucheria*, the green felt, is a very common alga, forming mats of coarse filaments on the muddy bottom of shallow pools and ditches. Some species are terrestrial and may often be found as thread-like growths over the damp earth of flowerpots in greenhouses. The filaments are long and sparingly branched, and are, of course, continuous tubes without cross walls except where reproductive organs are developed. Immense numbers of small, disk-shaped chloroplasts (Fig. 189, *F*) are present in the layer of protoplasm under the cell wall, and the very small nuclei lie among them. The protoplasm contains numerous globules of oil, which in this plant takes the place of starch as the first visible product of photosynthesis.

The zoöspores of *Vaucheria* are very large, many-nucleate and many-ciliate structures, visible to the naked eye. They are developed singly in terminal cells (sporangia), which are cut off at the ends of the filaments by the formation of a cross wall (Fig. 189, *A*). The protoplasm in the sporangium contains hundreds of nuclei from the beginning, and pairs of cilia are formed all over the surface of the protoplast opposite them (Fig. 189, *C*). The entire mass of protoplasm then slips out from the end of the sporangium (Fig. 189, *B*) and swims slowly away, but soon comes to rest and puts forth one or more filaments (Fig. 189, *D*). The nuclei and pairs of cilia in this interesting zoöspore of *Vaucheria* unquestionably represent the two-ciliate zoöspores characteristic of most of the *Siphonales* and the green algæ in general. The protoplasmic divisions necessary to cut out the numerous zoöspores in a sporangium are

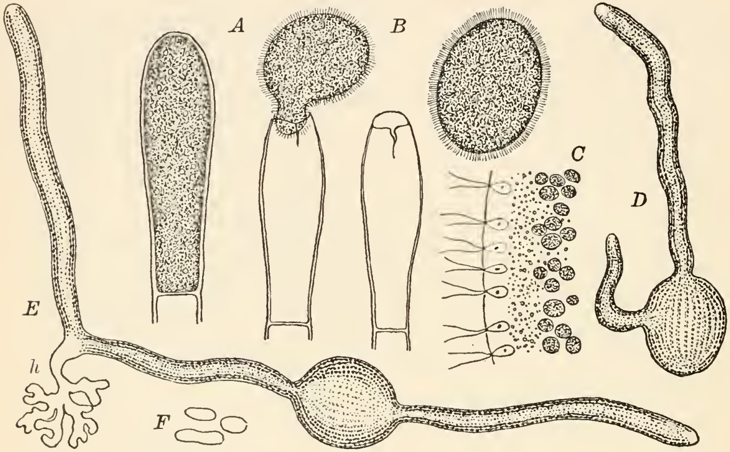

Fig. 189. Asexual reproduction of the green felt (*Vaucheria*)

A, formation and discharge of the large, many-ciliate zoöspore from the terminal sporangium; *B*, the zoöspore showing the ciliated surface; *C*, section through the surface of the zoöspore showing the pairs of cilia above the nuclei and the layer of plastids beneath; *D*, germination of zoöspore; *E*, young plant of *Vaucheria*, the two filaments having arisen at opposite ends of the zoöspore, one having developed an organ of attachment or holdfast *h*; *F*, a group of plastids, the lower in process of division. — *A*, *B*, after Götz; *C*, after Strasburger; *D*, *E*, after Sachs suppressed in *Vaucheria*, so that the entire mass of protoplasm remains together as a many-nucleate and many-ciliate unit, which is really a protoplast or cell in spite of its complicated structure. Some authors have regarded this zoöspore as a compound structure,—that is, a mass of small, two-ciliate zoöspores,

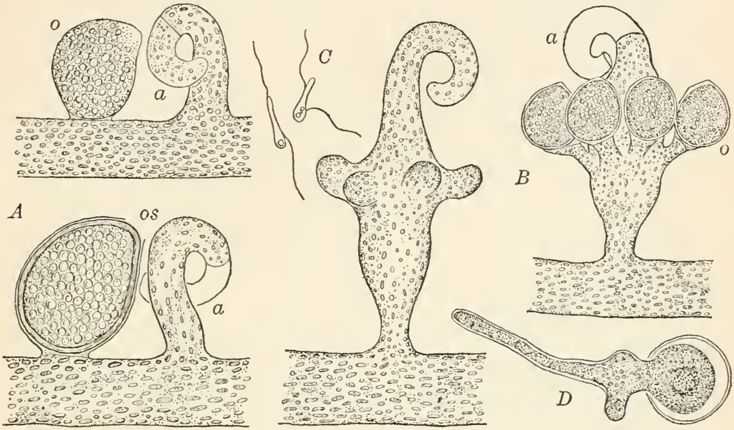

Fig. 190. Sexual reproduction of the green felt (*Vaucheria*)

A, *Vaucheria sessilis*; *o*, oögonium; *a*, antheridium; *os*, the thick-walled oöspore, and beside it an empty antheridium; *B*, *Vaucheria geminata*, a short lateral branch developing a cluster of oögonia and a later stage with mature oögonia *o* and empty antheridium *a*; *C*, sperms; *D*, germinating oöspore.—*C*, after Woronin; *D*, after Sachs

—but it is more correct to consider it a large, undivided, many-nucleate protoplast.

The sexual organs of *Vaucheria* are oögonia and antheridia, sometimes found side by side, as in *Vaucheria sessilis* (Fig. 190, *A*), and sometimes in groups on special side branches, as in *Vaucheria geminata* (Fig. 190, *B*). The oögonium is a large oval cell separated from the parent filament by a wall, and each develops a single egg (Fig. 190, *A, B, o*). The young oögonium contains numerous nuclei, but all of these degenerate except one, which lies near the center of the cell and becomes the single nucleus of the egg. The antheridium is a cell formed

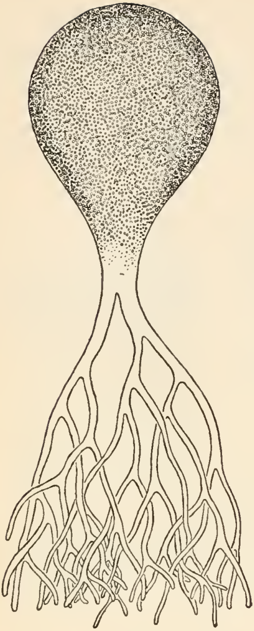

FIG. 191. *Botrydium* and *Protosiphon*

These forms of the siphon algæ are almost indistinguishable in the vegetative condition. The plants are little green globes, somewhat larger than pin heads, attached to the surface of mud and wet earth by a branching system of filaments (rhizoids). These single cœnocytic cells are therefore differentiated into a green part above ground, exposed to the air and sunlight, and a colorless underground portion in contact with moisture. A single cell may thus show the same relation of parts as a complex plant with aërial stems and leaves and a subterranean root system.

at the end of a branch, which is generally bent like a crook (Fig. 190, *A*, *B*, *a*), and discharges a very large number of small, two-ciliate sperms (Fig. 190, *C*). The sperms enter the oögonium through a pore in the beak-like extension at one side, and one of them, fusing with the egg, fertilizes it. The fertilized egg surrounds itself at once with a heavy wall, becoming an oöspore (Fig. 190, *A*, *os*), which is a resting spore in this form, as in *Volvox*, *Œdogonium*, *Coleochæte*, etc.

Vaucheria has been made the subject of some interesting experimental studies on the conditions which determine the formation of zoöspores and sexual organs respectively. Zoöspores are generally developed at once, following some marked change in the external conditions, as in the character of the water, or an increase in light exposure, or a rise in temperature. Sexual organs are formed when plants are cultivated in a 2–5 per cent solution of cane sugar at a fairly high temperature (50°–68° F.; 10°–20° C.), and in the presence of light. The conditions in *Vaucheria* probably illustrate very well the kinds of influences which cause an alga to begin its various forms of fructifications, but very few algæ have been studied in detail.

229. The cœnocyte. The large, many-nucleate structures called *cœnocytes*, so well illustrated by the siphon algæ and such fungi as the molds (Sec. 261) and water molds (Sec. 262), are peculiar to plants. The question may be asked, Why are cœnocytes considered single cells, and not a compound structure made up of a united mass of protoplasts represented by the numerous nuclei? It is known that the nuclei do not occupy fixed positions in the cœnocytes, as if they represented the cells of a compound structure. On the contrary, they shift with the movements of the protoplasm which behaves *as a unit*, like a gigantic protoplast growing in different directions in obedience to various stimuli, and carrying on the usual cell activities. For these reasons the cœnocyte must be regarded as a many-nucleate cell and not a compound structure or mass of protoplasts.

ORDER 6. THE STONEWORTS, OR *CHARALES*

230. The stoneworts.* The stoneworts (order *Charales*) are the most complex of the green algæ. The plant body (Fig. 192, *A*) consists of long, jointed stems, which bear circles of lateral branches at the joints. The sexual organs (Fig. 192, *B*, *C*, *D*) are borne on these branches, but are too complicated for consideration here. Many of the *Charales* are heavily incrusted with lime, which peculiarity gives them their popular name of stoneworts. They sometimes grow in great masses attached to the bottom of ponds and shallow lakes.

Some forms of stoneworts (*Nitella*), which are free from incrusting lime, frequently illustrate very beautifully the movements of protoplasm in the large cells (internodes) which lie

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* TO THE INSTRUCTOR: The *Charales* is such a highly special group that it is hardly wise to give it much attention in a general course, especially if time and material is available for a more thorough study of the *Confervales*. Nevertheless, material of the stoneworts is frequently easily obtained, especially in the Middle West, where it is difficult to do justice to the brown and red algæ, and it might be substituted for certain work in those groups. One of the best accounts of the *Charales* will be found in Goebel, *Outlines of Classification and Special Morphology of Plants*.

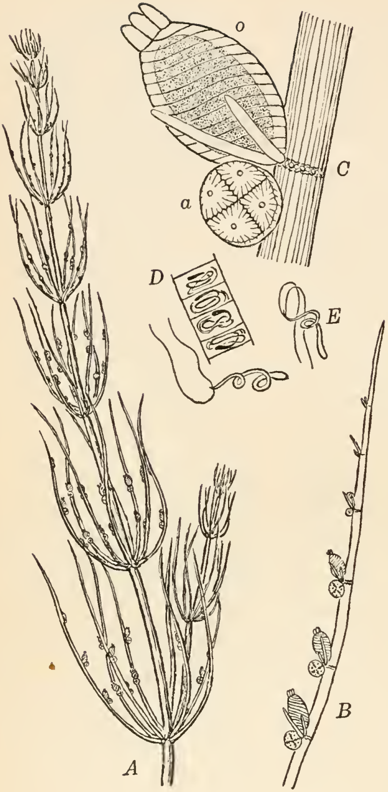

FIG. 192. The stonewort (*Chara*)

A, portion of plant showing circles of lateral branches at the joints (nodes); *B*, a lateral branch bearing the sexual organs; *C*, the sexual organs; *o*, oögonium, with spirally wound filaments encircling the egg and forming a crown above; *a*, the antheridium, composed of eight flattened cells (shields), inclosing the antheridial filaments; *D*, portion of an antheridial filament, each cell developing a single sperm; *E*, two-ciliate sperms

between the circles of lateral branches. The protoplasm passes in two streams in opposite directions somewhat diagonally around the cell. The edges of the stream form a line of stationary protoplasm (free from chloroplasts), because the movements of the currents, which may be seen on either side of the line, neutralize one another.

The *Charales* stand entirely by themselves at the end of a line of ascent whose developmental history is a mystery. They are very far above most of the green algæ in the complexity of the plant body and sexual organs, which are not, however, like those of the liverworts and mosses. The antheridium of the stoneworts is a very puzzling structure but the oögonium is easily understood. The jointed stems with circles of lateral branches are, of course, much more complicated than the typical thallus, but the simple life history, with no trace of an alternation of generations, makes it necessary to include them among the thallophytes.

Summary of the Green Algæ

231. Summary of the green algæ. The green algæ comprise a number of well-defined groups which are evidently widely separated from one another. The most conspicuous of these are the *Volvocaceæ,* the desmids and pond scums, the diatoms, the siphon algæ, and the stoneworts. They constitute independent evolutionary lines of varying importance, but each one clearly developing in ways peculiar to itself and quite apart from the theoretical main line of ascent to the liverworts and mosses (*Bryophyta*). A discussion of the origin of these groups and their possible relationships to one another would be much too complicated for the present account. The forms of the green algæ which seem to be nearest to the main line of ascent are in certain related families (*Ulothricaceæ, Chætophoraceæ,* and *Coleochætaceæ*), but it is very doubtful if any of them are directly on the main line, and there are no living algæ known which show clearly the origin of the bryophytes.

Almost all of the green algæ at some stage in their life history form zoöspores or motile gametes (the sperm being motile in heterogamous forms). These ciliate cells point clearly to an ancestry of the green algæ from groups comprising one-celled motile organisms something like the flagellates (Sec. 204) and lower forms of the *Volvocaceæ* (Sec. 215). The formation of the zoöspore and the motile gamete is considered to be a return in the life history, for a short time, to the primitive one-celled conditions from which the various lines of the green algæ are believed to have arisen. The motile conditions which occupy practically all of the life history of the flagellates and *Volvocaceæ* become reduced to a short reproductive period in most of the green algæ. The most important forward steps in the evolution of the green algæ came with the introduction of long vegetative periods in the life histories when the protoplasts remained quiet and formed many-celled plant bodies (cœnocytic siphon algæ excepted) of various structure. All the possibilities of development into such complex attached organisms as the higher spore plants and seed plants were determined by those changes in the habits of algæ by which the motile periods in the life history became reproductive stages, and the quiescent conditions came to be the conspicuous part of the life history as the vegetative plant body was gradually developed.

232. Summary of the reproductive organs and processes of the green algæ. *Zoöspores,* also called *swarm spores,* are ciliate asexual cells (generally two- or four-ciliate), and are developed as a rule numerously (in some forms singly, or in twos, fours, etc.) in a mother cell called a *sporangium,* or *zoösporangium.*

Gametes are sexual cells. The simplest forms are ciliate and have the same form and structure (morphology) as the zoöspores, to which they are related. These in the process of sexual evolution became differentiated into *eggs* and *sperms.* Gametes are developed in cells called *gametangia.*

Eggs are never ciliated, and are consequently nonmotile. They are generally large cells, with abundant chromatophores and food material. Eggs are formed in cells called *oögonia.*

Sperms, frequently called *antherozoids* by botanists, are always ciliated in the green algæ and are very actively motile. They are smaller than zoöspores and colorless, or almost colorless. Sperms are developed in cells called *antheridia,* or a group of such cells is frequently termed an *antheridium.*

Isogamy is the sexual condition in which the gametes are similar in form and structure; that is, they have the *same morphology.* They may differ in size. The sexually formed cell is called a *zygospore.*

Heterogamy is the sexual condition in which the gametes are different in form and structure, as the sperm and egg, and therefore have a *different morphology.* They are always very unlike in size, but this does not make heterogamy, because morphology does not deal with *size* but with *form.* The egg is fertilized by the fusion and entrance of a sperm and thus becomes a *fertilized egg,* or, if it develops a protective cell wall, an *oöspore.*

PLATE IV. Rockweeds exposed at low tide

Most of the growth is *Fucus vesiculosus*, but some of it is *Ascophyllum nodosum*, shown in the lower part of the plate. — After F. Börgesen

CLASS III. THE BROWN ALGÆ, OR *PHÆOPHYCEÆ*

233. The brown algæ. The *Phæophyceæ* comprise a very rge assemblage of marine algæ, or seaweeds, called the brown lgæ because their chromatophores are colored brown instead of reen. The brown pigment, however, performs the same sort f work (photosynthesis) as the chlorophyll of the green algæ. he brown algæ can generally be recognized at a glance by eir color, but the group is really separated from all other lasses of algæ by certain peculiarities of structure, or morhology. The plant bodies in most of the forms are very much rger and more complex than those of any green algæ and freuently have a degree of differentiation quite above that of the ypical thallus. Indeed, some of the higher brown algæ have ell-defined stems fastened to the rocks by remarkable holdsts, resembling clusters of roots, and bearing expanded leafke structures of complex and striking forms. Certain types evelop swollen bladders, which contain considerable oxygen, iven off from the tissues, and serve to float parts of the plant the water. Besides the complexity of the plant body the rown algæ are also distinguished by peculiarities of the reprouctive organs that can only be understood through a study f types. Iodine is obtained from the ash of certain kelps and ckweeds. These larger brown algæ are also gathered from e rocks and beaches by the peasantry of certain European untries and by farmers on the New England coast and spread er farm lands to fertilize the soil.

234. Life habits. The brown algæ are most luxuriant in the lder waters of the oceans, where they form extensive growths long the coasts. Some of the larger forms, as *Fucus* and *scophyllum*, are known as rockweeds because they cover the cks between low and high tide marks with heavy fringes of rown vegetation (Plate IV). Other forms, known as the kelps, r devil's aprons, grow below or just at low watermark and someimes form large beds attached to the rocks. These larger types can withstand the beating of the heaviest surf because of their firm texture and strong holdfasts, and some of them grow on the most exposed points and reefs. There are, however, many smaller brown algæ, membranous and cord-like forms, and some delicate filamentous types (*Ectocarpus*) which are as simple as many green algæ and grow generally in rather quiet waters.

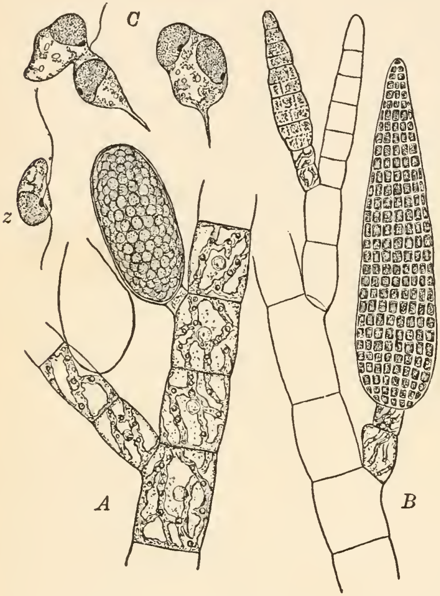

Fig. 193. A filamentous brown alga (*Ectocarpus siliculosus*)

A, unilocular sporangia, one containing zoöspores, the other empty; a zoöspore, *z*, shown at the left; *B*, plurilocular sporangia, the larger mature, the smaller still showing the outlines of the original cells in the branch from which it arose; *C*, the union of the gametes to form the zygospore; note that the chromatophores with the pigment spots remain separate. — *C*, after Oltmanns

We can only illustrate the brown algæ by representatives of three orders, — the *Ectocarpus* group, the kelps, and the rockweeds.

235. Ectocarpus. This alga (order *Ectocarpales*) is a branching filamentous type which forms tufts attached to the larger algæ, eelgrass, and to the woodwork of wharves. Its chief interest for us lies in the reproductive organs, which are of two sorts, and illustrate very well the reproductive processes of the lower brown algæ. The asexual organs are one-celled sporangia (Fig. 193, *A*), which develop large numbers of kidney-shaped zoöspores, each with a pair of cilia attached at the side (Fig. 193, *A*, *z*). Because the zoöspores are all developed in a single cell, the sporangia are called *unilocular* *sporangia*, to distinguish them from the sexual organs, but the structure is clearly the same as that of the one-celled sporangium of the green algæ.

The sexual organs are developed from side branches, most of whose cells divide repeatedly until an immense number of small compartments are formed. The filament thus becomes transformed into a complicated many-celled organ (Fig. 193, *B*) made up almost wholly of small cubical cells, each of which develops a single two-ciliate gamete similar to a zoöspore, or, perhaps, two or three of these motile elements. Because the gametes are developed in small compartments, the organ has been termed a *plurilocular sporangium.* It is clear that this many-celled organ is a very different sort of structure from the one-celled reproductive organs. It marks an important advance in the evolution of reproductive structures in plants and suggests the many-celled sexual organs characteristic of the bryophytes and pteridophytes.

The gametes are known to fuse in pairs (Fig. 193, *C*), as in many simple green algæ, and since they have a similar structure, the sexually formed cell is

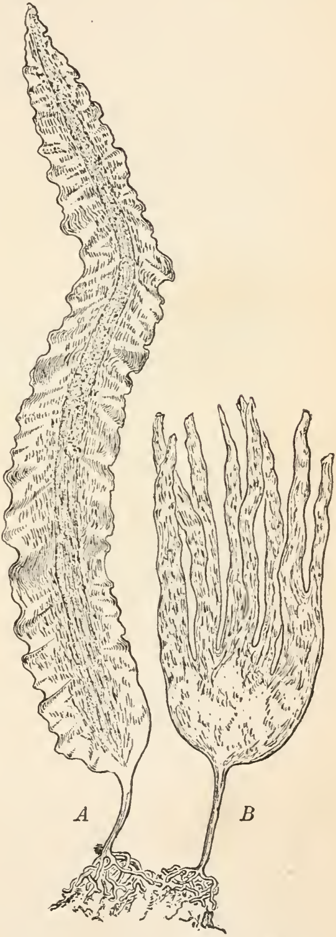

FIG. 194. Kelps from the North Atlantic

A, the simple type of *Laminaria*, some of whose species grow to be thirty or more feet long; *B*, the digitate type (*Laminaria digitata*), which is never very long, but is broad at the base a zygospore and the sexual condition is that of isogamy. It is interesting to note that these motile cells sometimes germinate without conjugation, just like the zoöspores which they resemble, — a fact which shows that sexuality has not become very firmly established in the simplest of the brown algæ and illustrates, as in *Ulothrix* (Sec. 217), the general conditions which are to be expected with the origin of sex in any group of plants.

236. The kelps. The kelps (order *Laminariales*), also known as the devil's aprons, are the largest types of the brown algæ. Those of the North Atlantic coast have comparatively simple forms (Fig. 194). There is always a *stalk* (stipe) attached to the rocks by a *holdfast* consisting of a cluster of strong outgrowths, and the stalk bears a long, leaf-like expansion called the *blade*. The blades of some kelps are divided lengthwise into segments, as in *Laminaria digitata* (Fig. 194, *B*).

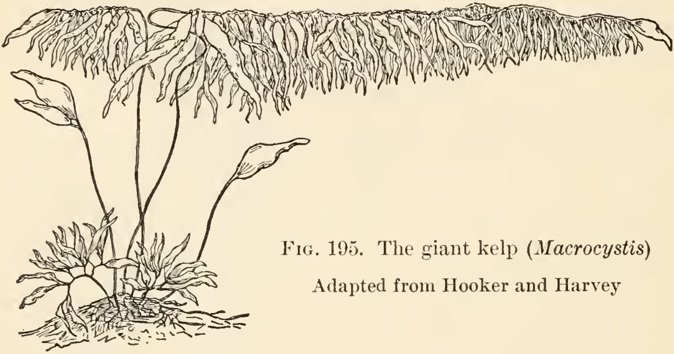

Fig. 195. The giant kelp (*Macrocystis*)
Adapted from Hooker and Harvey

Certain kelps of the Pacific coast are much more complex, consisting of numerous large, leaf-like blades variously arranged on different forms of stems. Some of the stems attain great lengths. Thus the giant kelp (*Macrocystis*, Fig. 195) has been reported six hundred to nine hundred feet long, which is two or three times the height of the giant redwoods of California. The sea otter's cabbage (*Nereocystis*, Fig. 196) frequently has a stem more than one hundred feet long, which is enlarged above into a hollow float that rests on the surface of the water and bears a number of strap-shaped leaves. The sea palm (*Postelsia*, Fig. 197) is another remarkable form, with a thick, strong stalk about a foot high, which bears a crown of small leaves and somewhat resembles a palm tree in miniature. *Macrocystis* and *Nereocystis* grow in deep water, but the sea palms are found on the rocks, where the surf breaks so heavily that the tough elastic stems are bent over at right angles by the force of every wave.

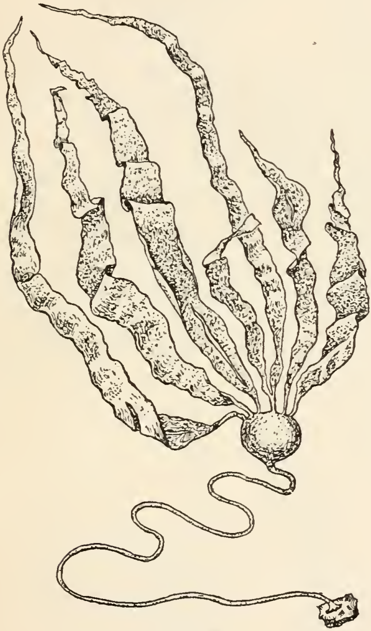

Fig. 196

Fig. 197

Fig. 196. The sea otter's cabbage (*Nereocystis*)
Adapted from Postels and Ruprecht

Fig. 197. The sea palm (*Postelsia*)

The kelps reproduce by zoöspores developed in one-celled sporangia that are formed in large patches upon the leaves.

There is no method of sexual reproduction known, and this is remarkable, for groups as highly developed and eminently successful as the kelps almost always have well-established and complex methods of sexual reproduction.

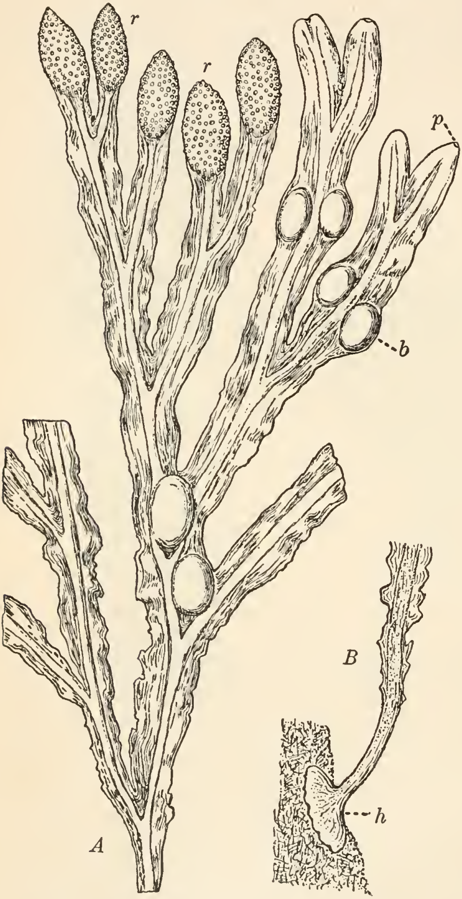

FIG. 198. A rockweed (*Fucus vesiculosus*)

A, habit sketch, showing the forking of the branches; *b*, air bladders; *r*, swollen fruiting tips (receptacles), with the sunken cavities (conceptacles) which contain the sexual organs; *p*, pit at a growing point. *B*, base of a plant; *h*, holdfast

237. The rockweeds. The rockweeds (order *Fucales*) are the highest forms of the brown algæ, both in vegetative structure and because of the complex sexual conditions (heterogamy), with characteristic eggs and sperms.

The commonest genus is *Fucus* (Fig. 198), which is very widely distributed in the colder seas and forms the bulk of the algal vegetation between tide marks (Plate IV). The plant body of *Fucus* forks very regularly (dichotomous branching), and the growth is from a region of cells situated in a pit at the end of each branch (Fig. 198, *p*).

The sexual organs arise from the sides

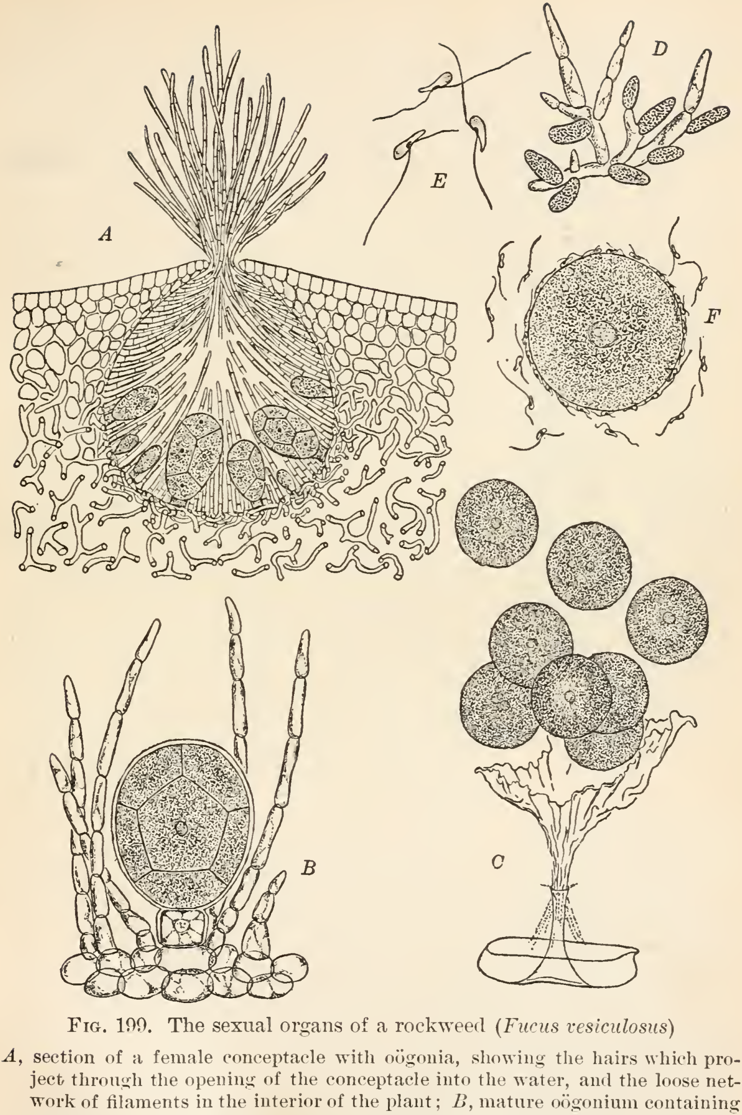

FIG. 199. The sexual organs of a rockweed (*Fucus vesiculosus*)

A, section of a female conceptacle with oögonia, showing the hairs which project through the opening of the conceptacle into the water, and the loose network of filaments in the interior of the plant; *B*, mature oögonium containing eight eggs; *C*, the discharge of the eggs from an oögonium; *D*, a group of antheridia on the branching filaments which grow in tufts over the sides and bottom of the male conceptacles; *E*, sperms very highly magnified, showing elongated form and the two cilia at the side; *F*, an egg lying free in the water and surrounded by sperms. — *B*, *C*, *D*, *E*, *F*, after Thuret and bottom of small cavities, called *conceptacles* (Fig. 199, *A*), which are developed in swollen tips of older branches termed *receptacles* (Fig. 198, *r*). Some species of *Fucus* (as *F. edentatus*) have both male and female organs in the same conceptacle, but in other species they are formed in different conceptacles, and even upon different plants, as in *F. vesiculosus*. The female organ is a large cell, or oögonium (Fig. 199, *B*, *C*), which in *Fucus* develops eight eggs. The male organs, antheridia, are also single cells (Fig. 199, *D*), but they are generally borne in dense clusters upon branching stalks, and each produces more than a hundred very small sperms with two cilia at the side (Fig. 199, *E*). The eggs and sperms are forced out of the conceptacles by the swelling of mucilage that is developed within the structure, aided by the contraction of the tissue when the plants are exposed at low tide to the drying action of the air.

FIG. 200. *Sargassum Filipendula*

Tip of plant showing leaf-like lateral branches, the stalked, berry-like, hollow floats, and the fruiting branches, or receptacles, *r*

The eggs are fertilized in the sea water outside of the conceptacles. The sperms gather around an egg in great numbers (Fig. 199, *F*), making it revolve, and finally one enters. The male nucleus passes rapidly to the center of the egg and in a few minutes begins to fuse with the female nucleus. The striking differences in size and structure between the large egg and minute sperm make the sexual process of *Fucus* one of the best illustrations of heterogamy in the plant kingdom. Such fertilized eggs as are fortunate enough to find favorable resting places begin to germinate within twenty-four hours, and develop directly into young *Fucus* plants.

238. Sargassum. *Sargassum* (Fig. 200) is one of the *Fucales* that deserves special mention for the complexity of its plant body, which bears three forms of lateral structures: (1) thin, leaf-like branches which resemble foliage, (2) berry-like floats, and (3) small reproductive branches, or receptacles (Fig. 200, *r*). Some species of *Sargassum*, when torn away from their attachment to rocks, are able to vegetate in the open sea, where they are called *gulf weed*, but they are not known to fruit in the free floating condition. Certain ocean currents carry and accumulate immense quantities of this floating gulf weed in great eddies in the ocean, forming the Sargasso seas.

239. Summary of the brown algæ. The *Phæophyceæ* stand entirely apart from the green algæ as a side line of plant evolution. There is much evidence that it is a group of very ancient origin, probably arising from an ancestry of motile organisms (somewhat like the flagellates) just as did the green algæ in early geological ages. The brown algæ have developed in their own peculiar ways the largest and most complex forms of plant bodies in the thallophytes, and also some very high types of sexual reproduction. It is clear, however, that these have no relation to higher plants, bryophytes and pteridophytes, and are also entirely independent of other groups of algæ. Thus heterogamy in the brown algæ has been developed entirely independently of heterogamy in the green algæ, illustrating very well how similar results may be worked out through different evolutionary lines independently of one another.

CLASS IV. THE RED ALGÆ, OR *RHODOPHYCEÆ*

240. The red algæ.* The *Rhodophyceæ* include the most beautiful of the marine algæ, for many of the forms are exquisitely colored in clear shades of red, and are extremely delicate in structure. Other forms are brownish red or purplish, and certain types are greenish. The pigment is held in chromatophores,

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* To the Instructor: In a brief course where only one type can be studied in the laboratory, *Nemalion* or *Batrachospermum* is preferable, followed by a study of the life habits of the group and demonstrations of herbarium material.

and performs the photosynthetic work of the plant. Although the red algæ can generally be distinguished by their color, the fundamental characters of the group are based on the structure of the sexual organs and certain complications in the life histories which will be explained in the accounts of *Nemalion* and *Polysiphonia*. The plant body of the red algæ ranges from filamentous types of great delicacy (as *Callithamnion*) to such coarse forms as the Irish moss (*Chondrus*) and the dulse (*Rhodymenia*). It is a remarkable fact that the large types are really composed of complicated systems of filaments so closely associated, however, as to give the appearance of a cell tissue. Adjacent cells in the same filament are usually connected by strands of protoplasm, a striking feature of the group. Some of the red algæ, as the Irish moss and the dulse, are eaten, and a number of them are used as relishes by the natives of the Hawaiian Islands, China, and Japan. Certain forms have an economic value for gelatin, which is obtained from their tissues; thus agar-agar comes from the stems of a red alga (*Gracilaria*) which grows in the seas of the Orient.

Fig. 201. The Irish moss (*Chondrus crispus*)

About one half natural size; the shaded spots are sexually formed fruits, or cystocarps

241. Life habits. The life habits of the red algæ are in striking contrast to those of the brown. They prefer warmer waters, and the best displays are on such coasts as the Mediterranean, the islands of the West Indies, southern California, and Australia. They generally flourish in deeper waters than the green and brown algæ, and form the greater part of the seaweed growth below the fringe of green and brown which is frequently quite conspicuous on rocks near low-water mark. Some of the forms are found at depths of two hundred feet or more, the depth limit varying with the clearness of the water. Most of the red algæ seem to prefer shaded situations among the rocks, and it is probable that their characteristic color is associated with these peculiar subdued light relations, so different from those of other algæ. Some types are incrusted with lime and form the curious growths on rocks called *corallines.*

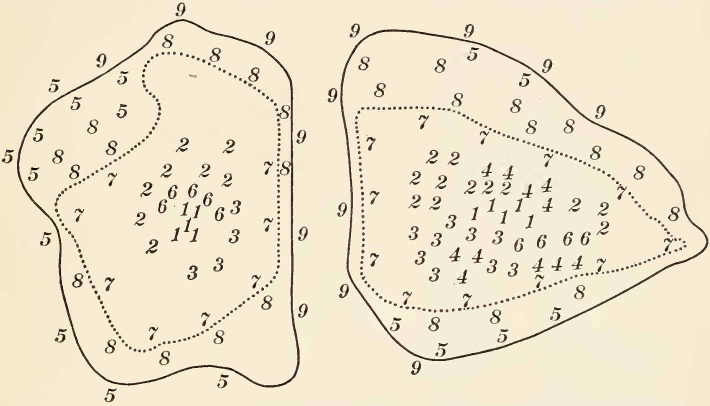

Fig. 202. The distribution of conspicuous algæ on two rocks of Spindle Ledge, Woods Hole, Massachusetts, in September, 1905

The dotted line is low-water mark, and the rocks are completely covered at high tide. Blue-green algæ: 1, *Calothrix scopulorum*, on the highest part of the rock. Green algæ: 2, *Ulva lactuca* var. *rigida* (sea lettuce); 3, *Enteromorpha prolifera* (sea lettuce); both forms grow well above low-water mark. Brown algæ: 4, *Fucus vesiculosus* (rockweed), in patches, but not plentiful in the summer; 5, *Chordaria flagelliformis* (shoestrings), heavy growths, well below low-water mark. Red algæ: 6, *Nemalion multifidum*, on the higher parts of the rock; 7, *Ceramium rubrum*, a well-marked fringe at low-water mark; 8, *Polysiphonia violacea*, a well-marked fringe just below low-water mark; 9, *Chondrus crispus* (Irish moss), large patches from one to three feet below low-water mark

242. The distribution of algæ on rocks. Many seaweeds are only found in certain situations upon rocks, where they grow in patches and fringes, and frequently exhibit a sort of zonation somewhat similar to the distribution of plant life around the margins of ponds and lakes. Fig. 202 presents a diagram of such distribution on two isolated rocks. It will be seen that there is a clear zone of a red alga (*Polysiphonia*) just below low-water mark, another zone (*Ceramium*) at or a little above this mark, while the Irish moss grows at some depth. The sea lettuces and rockweed are well above low-water mark, as is also *Nemalion,* which is exceptional in its habits for a red alga. On the northerly New England coast and beyond there are usually two distinct zones on the rocks, — one well above low-water mark, composed chiefly of rockweeds, and the other near this point, but below, and made up mostly of Irish moss with other red algæ, including the dulse.

243. Nemalion. *Nemalion* illustrates excellently the structure of the sexual organs and the sexually formed fructification of the red algæ, called the *cystocarp* (meaning a fruit cavity). The plant body is a rather soft, cord-like, branching structure, composed of an immense number of filaments held together by a stiff gelatinous substance around the cells. There is a central axis of delicate threads, while the outer regions consist of short filaments pointing outward. The cells of the outer filaments contain each a single chromatophore, and the vegetative activities (photosynthesis) as well as the reproductive take place in this region of the plant.

The male organs, or antheridia, consist of clusters of small cells at the surface of the plant (Fig. 203, *A*), each of which develops a single sperm, spherical in form and *without cilia,* and consequently *nonmotile.* The female organ (Fig. 203, *B*) is developed at the end of a short branch and consists of a cell which bears a long, hair-like extension called the *trichogyne* (meaning female hair), which is the receptive organ for the sperms. The sperms are applied to the trichogynes largely by the contact of male plants with the female as they are washed about by the movements of the water. When a sperm fuses with the trichogyne its nucleus (male) passes down into the swollen base of the female cell and unites there with a female nucleus. The trichogyne then withers above the fertilized female cell. The female cell is called the *carpogonium*, but it corresponds exactly to an oögonium, and indeed resembles very closely the oögonium of some species of *Coleochæte* (Sec. 222). Its peculiar form, with a receptive organ, the trichogyne, is undoubtedly associated with the nonmotile habits of the sperms. The red algæ are clearly heterogamous in their methods of sexual reproduction.

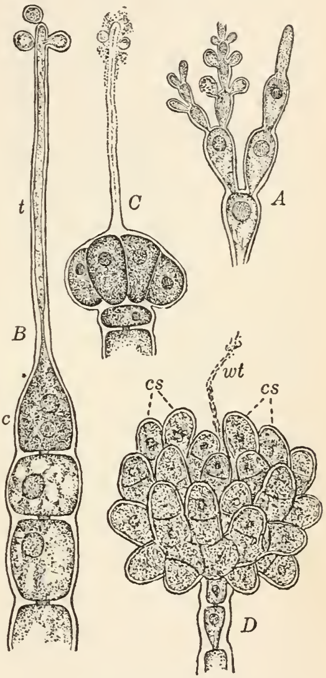

Fig. 203. *Nemalion multifidum*

A, antheridia, consisting of groups of small cells, each of which develops a single sperm; the vegetative branch at the right illustrates the method of terminal growth and the protoplasmic connections between the cells. *B*, the female cell, or carpogonium, *c*, with its trichogyne, *t*, to which are attached three sperms. *C*, early stage in the development of the cystocarp; the trichogyne above has begun to wither. *D*, mature cystocarp composed of fertile filaments which develop the carpospores *cs* terminally; *wt*, withered trichogyne

The female cell, or carpogonium, after fertilization, gives rise to a dense cluster of short filaments, called fertile filaments, which all together form a globular fructification called the *cystocarp* (Fig. 203, *D*). The terminal cells of the fertile filaments become spores, termed *carpospores*, which develop new *Nemalion* plants. The cystocarp is clearly a new type of fructification in the algæ. It is a structure which begins with the fertilization of the carpogonium and ends with the formation of carpospores, and thus stands as a phase in the life history inserted between two generations of the sexual plants.

244. Batrachospermum. *Batrachospermum* is one of the few fresh-water forms of the red algæ, and is also an exceptional type for its color, which is generally some shade of green. The sexual organs and cystocarps are enough like those of *Nemalion* to make it as good a form to illustrate the sexual processes and life history of the red algæ as the latter type, and it is sometimes more available for inland classes. *Batrachospermum* grows in clear brooks and is generally found in its best condition in late winter and early spring.

245. Polysiphonia. *Polysiphonia* illustrates some further complexities in the life history of the red algæ which are not present in *Nemalion* and *Batrachospermum.* The filaments of these beautiful plants consist of rows of cells, called *siphons,* connected with one another in an elaborate manner. There is a central siphon, around which are arranged a circle of outer siphons variable in number for different species.

The sexual organs are found on separate plants. The male organs, antheridia, are modified branches (Fig. 204, *A*) that develop an outer covering of small cells which form the sperms (Fig. 204, *B*). The female organ is found on a small branch (Fig. 204, *C*) and consists of a carpogonium, with its trichogyne, accompanied by a number of vegetative cells which later take part in the development of the cystocarp. The fusion of a sperm with the trichogyne fertilizes the carpogonium as in *Nemalion.* There are two sets of activities concerned with the development of the cystocarp: (1) there are some remarkable cell unions between the fertilized carpogonium and neighboring cells (auxiliary cells) for nutritive purposes, and then the development of carpospores from the large fusion cell which is formed; (2) accompanying this activity there is the development of an urn-shaped envelope (Fig. 204, *D*), from some of the vegetative cells around the carpogonium, and this is clearly a protective structure to contain the carpospores. The first set of activities corresponds to the development of the simple cystocarp of *Nemalion.* The second set forms the additional urn-shaped protective case. The cystocarp of *Polysiphonia* is therefore a system of two tissues, one derived from the fertilized carpogonium, and the other from the vegetative cells of the parent plant.

Besides the sexual plants (male and female) there is an asexual condition in *Polysiphonia* called the *tetrasporic plant.* Tetrasporic plants are individuals which develop asexual spores, called *tetraspores* because they are formed in groups of four, termed *tetrads,* in mother cells (Fig. 204, *E, F*). The tetraspore mother cells arise from the central siphon near the ends of the branches.

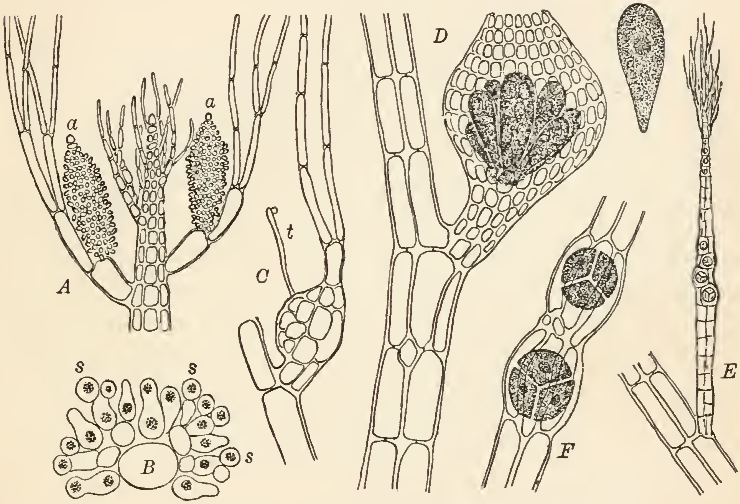

FIG. 204. *Polysiphonia violacea*

A, tip of filament showing two antheridia, *a*; *B*, cross section of a portion of an antheridium illustrating the development of the sperms at the ends of the very numerous short branches; *C*, a procarp with the projecting trichogyne *t*, from the female cell (carpogonium), which is hidden by the surrounding sterile cells; *D*, mature cystocarp with the urn-shaped envelope inclosing the cluster of carpospores, a single spore shown at the right; *E*, a short branch from a tetrasporic plant; *F*, two groups of tetraspores from a branch similar to *E*; note the peculiar arrangement of the tetraspores in a group of four, or tetrad

Some recent investigations clearly indicate that the tetrasporic plants come from carpospores, and that the tetraspores develop into sexual plants. So there is an alternation of sexual and tetrasporic plants in the life history of *Polysiphonia.*

246. Summary of the red algæ. It is quite certain that the red algæ have had their origin from a very much higher level than the green or brown algæ because of the complicated sexual organs and life histories and the absence of motile stages represented by the zoöspores and motile gametes of those groups. The red algæ resemble *Coleochæte* (Sec. 222) in a number of features, and it is possible that this type may be rather close to the starting point of the group. The peculiar structure of the female sexual organ (carpogonium), which is really an oögonium with a receptive organ (trichogyne), is undoubtedly associated with the loss of motility on the part of the sperms. But the most remarkable peculiarity is the development from the fertilized carpogonium of a tissue which produces carpospores. This structure (from the fertilized carpogonium to the carpospores) is a new phase in the life history of algæ, and together with protective envelopes, when present, constitutes the cystocarp. It is probable that the asexual tetrasporic plants found in most species of the red algæ arise from the carpospores, and that the sexual plants in these types are developed from the tetraspores. The structure developing from the fertilized carpogonium and ending with the carpospore, together with the tetrasporic plant, when present, therefore forms an asexual phase in the life history, alternating with the sexual plants. Such asexual phases are called *sporophytes* (meaning spore-bearing plants), to distinguish them from the sexual plants, called *gametophytes* (meaning gamete-bearing plants), and their following one after another in a life history constitutes an *alternation of generations.* Such an alternation of generations is found in very few groups of the thallophytes, but it is characteristic of the life histories of all higher groups beginning with the liverworts and mosses (Sec. 285). Its significance is discussed in Chapter XXVI.

CHAPTER XXI

SUMMARY OF THE LIFE HISTORIES AND EVOLUTION OF THE ALGÆ

247. The life histories of the algæ. The life history of a plant is the succession of stages leading from one generation to another and of course includes the reproductive periods. Reproduction may be as simple a process as the breaking off of portions from the parent plant, called *vegetative reproduction.* Almost all groups of plants have developed some forms of vegetative reproduction. The detached portions may be merely fragments, as in *Oscillatoria* (Sec. 209), or much more complicated, as certain bud-like structures in some of the brown and red algæ. Methods of vegetative reproduction give very simple life histories, which are merely a succession of similar forms such as may be represented by the formula

$$P - P - P - P, \text{ etc.,}$$

P standing for the plant type.

The commonest methods of reproduction in the algæ are through the special cells called spores, which may be asexual in character or formed sexually. The commonest form of *spore reproduction* in the algæ is through the zoöspore. When there is no sexual process in the life history, but some method of asexual spore reproduction, the formula of the life history becomes

$$P - asex.\ s. - P - asex.\ s. - P, \text{ etc.,}$$

asex. s. standing for asexual spore.

The development of sex in a plant complicates at once the life history. Gametes are formed, which unite to give sexually formed cells or spores. These spores may develop directly into plants like the parents, as in *Sphærella* and *Volvox, Spirogyra,* *Vaucheria*, *Chara*, and *Fucus*, or they may form zoöspores, which swim off and grow at once into plants like the parents, as in *Œdogonium*, *Ulothrix*, and *Coleochæte*, the latter type developing the zoöspores somewhat indirectly through a group of cells. But in all these forms the essentials of the life history are expressed by the formula

$$P < {}^{g}_{g} > \mathit{sex.\ s.} - P < {}^{g}_{g} > \mathit{sex.\ s.} - P,\ \text{etc.},$$

g and *sex. s.* standing for gamete and sexually formed spore, respectively.

It must always be remembered that the algæ with sexual methods of reproduction frequently have also asexual zoöspores or other forms of asexual reproduction, which may produce a number of successive generations between the development of sexual plants. This happens very frequently among the green algæ (as in *Ulothrix*, *Œdogonium*, *Coleochæte*, and *Vaucheria*) and in the lower brown algæ (as *Ectocarpus*). The life history formula of the sexual algæ may then be variously broken by the introduction of successive generations developed asexually.

In the red algæ the sexually formed cell corresponding to an oöspore does not give rise at once to a generation like the parent plant, but an asexual generation is inserted between successive sexual plants, alternating with them. This asexual phase may be represented by the tissue which produces the carpospores within the cystocarp, or it may be represented by this structure plus the tetrasporic plant. There is, then, in the red algæ an alternation of generations, an asexual phase, or *sporophyte* (the cystocarp and tetrasporic plant), alternating with the sexual plant, or *gametophyte*. This is the most complex type of life history in the algæ and may be expressed by the formula

$$G < {}^{g}_{g} > - S\left(\begin{array}{l}\text{cystocarp and}\\ \text{tetrasporic plant,}\\ \text{when present}\end{array}\right) - \mathit{asex.\ s.}\left(\begin{array}{l}\text{carpospore and}\\ \text{tetraspore,}\\ \text{when present}\end{array}\right)$$

$$- G < {}^{g}_{g} > - S - \mathit{asex.\ s.} - G,\ \text{etc.},$$

G and *S* standing for the gametophyte and sporophyte generations, respectively. It will appear later that the higher plants have essentially the same life history formula as this.

248. The evolution of sex. The account of the algæ has given material for a brief discussion of the origin and evolution of sex. It has been shown that the simplest forms of sexual cells, or gametes, have essentially the same structure and origin as the zoöspores. These conditions are illustrated by *Sphærella, Ulothrix, Ulva,* and *Cladophora.* The difference between the gamete and zoöspore is chiefly one of size. The gametes are smaller because they are generally formed more numerously in their mother cells. Gametes sometimes are able to germinate like zoöspores, but such gametes are apt to develop small and weak plants, and as a rule they must fuse with one another in pairs in order to live. It seems clear that sex arose with the development of a type of zoöspore smaller and apparently weaker in its power of vegetative growth than the normal zoöspore. These smaller zoöspores formed the habit of fusing in pairs, and this habit, finally becoming fixed in the plant's life history, developed into a method of sexual reproduction.

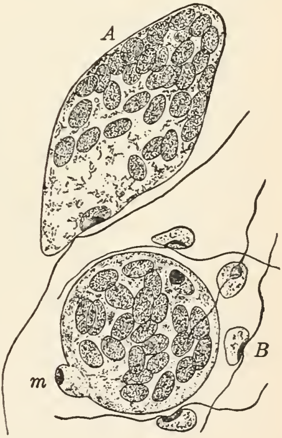

FIG. 205. *Cutleria multifida*

A, the large female gamete; *B*, the same at rest and surrounded by small male gametes, one of which, *m*, is shown in the act of fusion

After the establishment of sex in a group of plants, further developments will tend to modify the form of the gametes, the process finally ending in their differentiation into eggs and sperms. The simplest gametes are so similar in form and size that they cannot be distinguished as male and female, but a number of algæ have gametes which are different in size, although similar in structure, or morphology. This condition has been noted in species of *Chlamydomonas* (Fig. 177), and some other green algæ (as the siphon alga *Bryopsis*) show it, while among the brown algæ certain species of *Ectocarpus* and *Cutleria* (Fig. 205) furnish especially good illustrations. The larger gamete is female and often has a relatively short motile period, being fertilized when at rest by the smaller male gamete, thus resembling an egg (Fig. 205, *B*). These are transitional conditions leading towards the highest types of gametes, — the egg and sperm. The term *isogamy* (similar gametes) is applied to sexual conditions when the gametes are *similar in form,*— that is, have the *same structure,* or *morphology,* even though they may be very different in *size.* The sexually formed cell is called a zygospore.

Heterogamy (dissimilar gametes) is the sexual condition in which the gametes are *unlike in form,* — that is, have a *different structure,* or *morphology,* one being the larger nonmotile egg, and the other the small, specialized, motile sperm. The sexually formed cell is called an oöspore, or the egg is said to be fertilized after the union with the sperm. Several eggs may be formed in the mother cell, or oögonium, as in *Fucus,* but they are generally developed singly. This latter condition is the result of evolutionary processes by which all of the protoplasm and nutritive material in the oögonium is preserved for a single egg, thus giving it all the energy and power of growth possible. The sperms, on the contrary, are frequently developed in very great numbers in their parent cells, and are consequently small, and must die quickly if they are unable to fertilize eggs.

It is very important to note that the principles affecting the evolution of sex are always at work and have undoubtedly operated separately in various groups of plants. Thus heterogamy has developed independently in the lines of the green algæ, ending in *Volvox, Œdogonium, Coleochæte, Vaucheria,* and *Chara,* and in the rockweeds (*Fucales*) as well. Heterogamy is the highest point of sexual evolution, but plants above the thallophytes show some important advances in their methods of protecting the egg. It will appear later that the eggs of liverworts, mosses, and ferns are retained in special, protective, cellular structures called *archegonia*, which are the female reproductive organs. The presence of this organ is one of the important characters of these groups (bryophytes and pteridophytes), and its absence is one of the peculiarities of the thallophytes.

249. The evolution of the algæ. The evolution of the algæ is the result of many factors which affect their life habits and life histories. Sexual processes have been the chief factors modifying life histories, for they are always a stimulus to development, and have been the starting points for some of the most important complications in the life histories and developments of groups. The most conspicuous illustration of this principle appears in the red algæ, where an asexual generation follows the sexual process, and similar conditions are present in a peculiar group of the brown algæ represented by *Dictyota*.

One of the most clearly marked evolutionary principles illustrated in the algæ is the tendency to establish fixed or attached forms and to limit the motile stages in the life history to the reproductive cells (zoöspores or gametes). Some of the lower algæ are motile throughout almost all of their life histories, as in the *Volvocaceæ* (Sec. 215) and that group of uncertain relationships, the flagellates (Sec. 204). But the motile stages become merely reproductive phases in the higher forms. Thus the appearance of zoöspores and motile gametes in the life histories of higher types of algæ is believed to represent a return for a short time to the motile conditions and habits of their ancestors.

The establishment of attached plant bodies opened immense possibilities of plant development, and resulted at once in a great variety of structures. The first of these were simple forms of thalli, such as filaments, membranes, and plates of cells. But later the plant structures became more complex, developing holdfasts and stems, which bore leaf-like lateral structures, evidently differentiated to give a large exposure to sunlight, and for the work of photosynthesis. Thus types of plant bodies arose which were more complex than the thallus, since they showed three regions, — stems, leaf-like blades, and holdfasts. We shall see later that the stems, blades, and holdfasts of the highest algæ do not correspond to the stems, leaves, and roots of fern and seed plant, which developed very much later through a complicated history. But this differentiation of the plant body in the thallophytes is, at least, a response to the same sort of influences as guided the development of the higher plants. These influences were in part the evident advantages to a plant of being fastened to a suitable attachment, from which it can grow and present as much surface as possible to the sunlight.

In conclusion, one should think of the algæ as comprising a large number of divergent lines, whose relationships are sometimes so distant that one cannot make even a good guess as to the evolutionary history. The stoneworts (*Charales*) constitute perhaps the best illustration of such an isolated group. Very few of the algæ now living are near the theoretical main line of ascent to the liverworts and mosses. The algæ should be thought of as spreading out in many directions, each group developing in its own particular line of evolution, adjusting itself as best it may to its particular sort of life. Some possible relationships have been suggested in the accounts of the various groups, but the subject is too complex to be given detailed consideration here.

CHAPTER XXII

THE FUNGI AND THEIR RELATION TO FERMENTATION AND DISEASE

250. The fungi.* The fungi are thallophytes whose plant bodies have no chlorophyll or other coloring matter capable of doing the work of photosynthesis. Consequently fungi are unable to manufacture the primary foods of plants, such as starch, and are absolutely dependent upon organic substances obtained from animals and plants. Fungi must therefore live either as *parasites* upon living plants or animals, called their *hosts*, or as *saprophytes* (meaning decay plants) upon dead organic matter or the products of decay. Fungi are frequently spoken of as colorless plants, because they have no chlorophyll, but many forms are brilliantly colored by special pigments.

The fungi have undoubtedly been derived from the algæ,—not from a single group of the algæ, however, but from several widely separated groups. Consequently the classes of the fungi have not developed one from another, but in most cases are believed to be either of entirely independent origin or of very remote relationship through ancient forms of algæ no longer living. The chief peculiarities of the structures and life histories of fungi are largely the results of their adaptations to lives of parasitism or saprophytism. One of the results of these adaptations has been the development of a much greater number of species than is found in the algæ.

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* To the Instructor: As in the account of the algæ, this chapter describes more forms than should be given in a general course. Many of them must be omitted or merely discussed in the class. They have been included in order to provide a range of material for selection adaptable to various sections of the country and the different conditions under which the subject must be presented.

We shall consider five classes in the series of the fungi among the thallophytes (see Outline of Classification, p. 155).

Class V.	The bacteria, or *Schizomycetes.*
Class VI.	The yeasts, or *Saccharomycetes.*
Class VII.	The alga-like fungi, or *Phycomycetes.*
Class VIII.	The sac fungi, or *Ascomycetes.*
Class IX.	The basidia fungi, or *Basidiomycetes.*

CLASS V. THE BACTERIA, OR *SCHIZOMYCETES*

251. The bacteria. The bacteria are the smallest living beings known. The single cells of many species are less than one ten thousandth of an inch in diameter, and some are very much smaller still. Most of the bacteria are one-celled. Some types are spherical or oval, some are straight or slightly bent rods, and some are spirally twisted forms of various lengths (Fig. 206). Certain species are provided with numerous cilia and are actively motile. The cells may be loosely joined together in chains or collected in jelly-like masses or colonies, which are sometimes brightly colored, yellow, red, blue, or green. Some of the bacteria are filamentous and made up of rows of cells. The cells are very simple in structure, since they do not have a clearly defined nucleus, and in this important respect they resemble the blue-green algæ, from which they are believed to have been derived (Sec. 211).

The cells of the bacteria multiply by simply splitting apart, which gives them their name of *Schizomycetes*, or fission fungi. These cell divisions, under favorable conditions, take place in some forms as frequently as once every half hour, and the descendants from a single individual may number many millions in a few days. The bacteria are only limited in their remarkable powers of multiplication by lack of food or other unfavorable conditions. Many bacteria have the power of developing thick-walled resting cells, or spores, within the parent cell, which can survive a temperature above the boiling point of water and also

Fig. 206. Groups of bacteria stained to show their cilia

A, *Bacillus subtilis*, an organism of decay characteristic of hay infusions; *B*, *Bacillus typhi*, the germ of typhoid fever; *C*, *Bacillus vulgaris*, single cells and filaments; *D*, *Planococcus citreus*, which forms yellow colonies on various substrata; *E*, *Pseudomonas syncyanea*, which turns milk blue; *F*, other species of *Pseudomonas*; *G*, *Microspira comma*, the germ of Asiatic cholera; *H*, *Spirillum undula*, in water containing decaying fish, algæ, etc.; *I*, another species of *Spirillum*. — After Migula below freezing, and are able to live for very long periods. But other forms, as the *Bacillus* of typhoid fever (Fig. 206, *B*), may be certainly killed within a few minutes by boiling the water in which they live. Certain bacteria, as the species which produce lockjaw and cause butter to become rancid, will live without air, and are even injured by contact with free oxygen. They obtain the oxygen necessary for respiration from compounds, such as the carbohydrates, which contain it.

The bacteria are present almost everywhere, floating in the air on particles of dust, in the water, in the soil, and always living within and upon the bodies of animals. Thus the bacteria are ready to grow and multiply wherever they find favorable conditions, but these are exceedingly various for the different species. Some forms are restricted to a parasitic life on particular hosts, as certain animals or plants, or man. Other types are connected with special chemical reactions, as in the processes of decay, fermentation, nitrification, etc. Many bacteria are indispensable to life on the earth, and of the greatest service to man. Many forms are harmless, but of no special value to man. Some cause dangerous contagious diseases.

252. Decay. Decay is the destruction or decomposition of highly complex organic compounds, such as the proteids, fats, sugars, and cell walls of plants, by which they are broken down into successively simpler substances, and finally into fluids and gases, some of which are very ill smelling. The products of decomposition form various chemical combinations, and are finally used again in the constructive processes of life. The bacteria and other fungi are the chief agents of decay, and if it were not for them the world would soon be filled with organic waste products, together with the dead bodies of animals and plants of no value as food. Thus all the chemical elements capable of sustaining life would long ago have been used up and life on the earth would have ceased. The bacteria are therefore chiefly responsible for a circulation of elements (see diagram, Fig. 207), from the highly complex organic compounds of animals and plants back to the simpler substances from which green plants manufacture their food and build up protoplasm.

Food may be kept indefinitely when under conditions that hinder the growth of bacteria, as in cold storage. The exclusion of all bacteria from hermetically sealed tinned foods, in which all germs have been previously killed by heat, is the chief principle in the success of the canning industry. The agreeable flavors of high-grade butter and certain cheeses, as well as the gamy taste of meat, are largely due to bacteria, and really indicate the first stages in the process of decay, although usually not at all harmful or distasteful. Not infrequently, however, incipient putrefaction forms certain organic poisons, called *ptomaines*, in nitrogenous foods, and these may give rise to distressing symptoms, or even prove fatal to the consumer.

253. Fermentation. Decay may take place in two very different classes of substances: (1) the carbohydrates, such as cellulose, starch, sugar, etc., and (2) the proteids or nitrogenous substances that make up protoplasm, flesh, and many food products. The breaking down of the carbohydrates is called *fermentation,* and many other fungi besides the bacteria are concerned with the process. Yeasts, for example, are the most important organisms in the fermentation of sugar, and the decay of cell walls in timber is chiefly due to some of the higher fungi.

The best-known types of fermentation are the *alcoholic* and the *acid.* Alcoholic fermentation involves the change of sugars to alcohols, accompanied by the formation of large quantities of carbon dioxide, and will be considered more especially in the account of the yeasts. Acid fermentation is the transformation of sugars and alcohols into organic acids, and bacteria play the most important part in this process. Thus the change of cider to vinegar is one of sugars and alcohols into acetic acid, and the souring of milk is the formation of lactic acid from milk sugar. Both processes are caused by bacteria. There are a number of stages in the processes of fermentation. For example, cellulose is first changed into some kind of sugar, and this later into alcohols and organic acids. The last stages result in the formation of the gas carbon dioxide (CO_2) and sometimes marsh gas (CH_4), which, when mixed with hydrogen phosphide, becomes the "will-o'-the-wisp" of swamps.

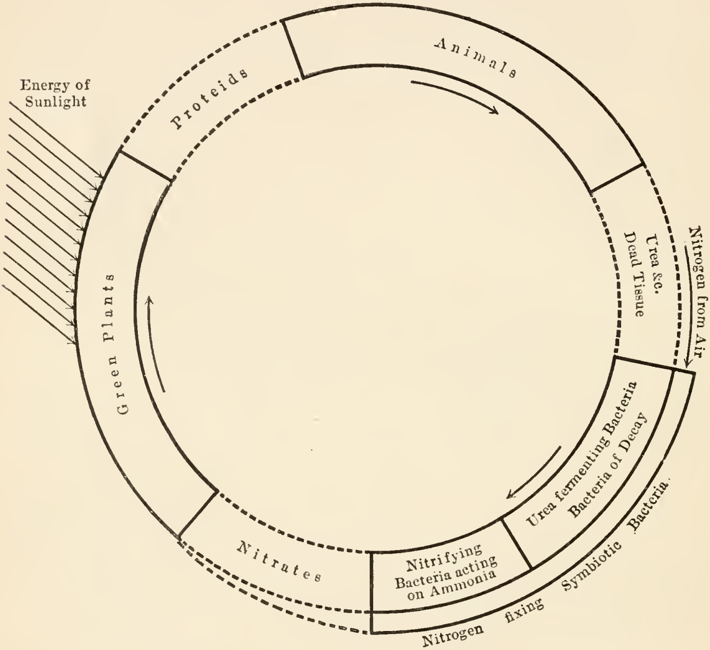

Fig. 207. Diagram illustrating the circulation of nitrogen

Nitrogen is taken by green plants from the nitrates, and through energy derived from the sunlight the proteids are formed. Animals carry the process of proteid manufacture somewhat farther. The nitrogen of the proteids is then returned, through the decay of waste products (urea, etc.) and dead tissues, to simpler substances, and finally to ammonia, which is worked over into nitrates by the nitrifying bacteria. Free nitrogen is brought into the circle by the nitrogen-fixing symbiotic bacteria

Some important forms of fermentation have no connection with living organisms, but are due to special substances called unorganized ferments, or *enzymes* (Sec. 10). Such a ferment is diastase, which converts starch to sugar.

254. Nitrification. The decay of proteid matter involves, first, the change of the insoluble proteids into soluble substances called *peptones,* — a similar process to that of digestion in the stomach. This liquefaction is due to the secretion of special ferments by certain bacteria. Then follow further complicated changes until the nitrogenous substances are broken down, and ammonia (NH_3), a relatively simple compound, is formed, together with various organic acids and other compounds. Two forms of bacteria which are abundant in almost all soils coöperate to transform the ammonia first into nitrous acid, and then into nitric acid, the latter forming at once *nitrates,* or salts of nitric acid. The nitrates are the chief source of the nitrogen supply of green plants. The process by which the ammonia of decay becomes available through the nitrates for plant use instead of passing into the air is called *nitrification.*

255. The circulation of nitrogen. There is a circulation of nitrogen in nature, which is indicated in the diagram (Fig. 207). This circulation starts with the nitrates, which are taken up in solution by the cells of green plants, — in the higher plants, of course, through the root system. The nitrogen in the nitrates is combined with carbon compounds obtained from the carbohydrate food manufactured by the processes of photosynthesis. Hydrogen, oxygen, sulphur, and often phosphorus also enter into the resultant substances, which are proteids. The energy which makes possible this building up of the complex proteids comes from the sunlight, as is indicated in the diagram. Animals are able to carry the building-up processes somewhat higher, obtaining their energy from food which comes directly or indirectly from plants. Then the breaking-down process begins through the decay of nitrogenous waste products and of dead matter, and this is accomplished as described in the previous sections through the activities of fungi and chiefly the bacteria. Finally, simple ammonia is produced, and this, by the process of nitrification, enters into the formation of nitrates, and the nitrogen is then available again for green plants.

256. The fixation of free nitrogen. One of the most important relations of bacteria to agriculture and to plant life generally lies in the ability of some species to put the free nitrogen of the air into chemical compounds that are available for absorption by green plants growing in barren soil. When crops are taken off the land through a series of years the supply of nitrates is largely used up and the soil becomes impoverished or exhausted. The nitrogen may be brought back to such soil by fertilizers, but this is expensive. The restoration of nitrogen to barren land has been one of the most serious problems of agriculture. There is one of the bacteria (*Pseudomonas radicicola*), which lives on the roots of members of the legume, or pea family, including such forms as the clover, alfalfa, and soy bean, and develops swollen regions called *root tubercles* (Fig. 208). This remarkable organism is able to take the free nitrogen from

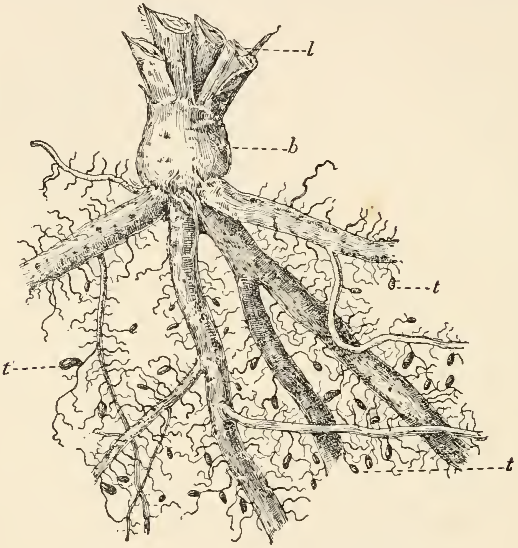

Fig. 208. Tubercles on the roots of red clover

l, section of ascending branches; *b*, enlarged base of stem; *t*, root tubercles containing bacteria the air and pass it through complicated chemical changes to the clover and alfalfa. Consequently these crops can be grown on worn-out soil or in waste land that is deficient in nitrates. Indeed, soils may now be inoculated with fluid cultures of these "nitrogen-fixing bacteria," so that the organisms will immediately establish root tubercles on the seedlings of these legumes, when sown, or the seeds themselves may be soaked in cultures insuring the application of the bacteria.[1] Therefore, when a soil becomes barren of nitrogen through successive crops of wheat, for example, the nitrogen may be largely restored by planting clover or alfalfa and plowing the crops under. Barren soil may also be inoculated more certainly by distributing over it earth from an old clover field.

The "nitrogen-fixing bacteria" make available the almost inexhaustible supply of free nitrogen in the air which cannot be absorbed by green plants and which consequently has been of no service to agriculture. As indicated in the diagram (Fig. 207), free nitrogen is constantly being brought into the nitrogen circle through the bacteria which form root tubercles (symbiotic bacteria), and this helps to make up the loss of nitrogen from the nitrogen circle, which comes in various ways, as by fire or the escape of ammonia into the air.

257. The germ diseases. There is a class of contagious, and in some cases very dangerous, diseases caused by certain bacteria which are frequently called microbes, or germs. The most serious are diphtheria, typhoid fever, tuberculosis (consumption), cholera, leprosy, bubonic plague, pneumonia, influenza or grippe, and whooping cough. Some other germ diseases, such as malaria, tropical dysentery, and possibly smallpox, are caused by lowly organisms which are not, however, bacteria. The germ diseases are due to the parasitic development of the organism within the

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[1] See Moore, "Soil Inoculation for Legumes," United States Department of Agriculture, Bureau of Plant Industry, *Bulletin 71*, 1905, and Wood, "Inoculation of Soil with Nitrogen-Fixing Bacteria," *Bulletin 72*, Part IV, 1905.

human or other host. They are contagious because the germs can be easily passed directly or indirectly in various ways from the ill person to those around him.

The active substances which affect the patient are known in all cases to be certain poisons called *toxins*, which are, for the most part, secretions, less often decomposition products, accompanying the growth of the bacteria. These poisons become distributed by the blood and cause the fevers. The body resists the effects of the toxins to the best of its ability, and in some cases substances are formed called *antitoxins*, which neutralize the poisons. The injection into the human body of an antitoxin, which is obtained from the blood of a horse infected with diphtheria, is the chief principle in the "antitoxin" treatment of this very serious disease. Recovery from a germ disease generally renders the person safe, or immune from further attack for a long time, because the body has developed resistant powers to the poisons and growth of that particular germ. The virulent poisons called ptomaines are usually the result of bacterial growths in foods that have not been properly kept.

Inflammation of wounds is caused by germs, and the formation of pus is in large part the gathering of white blood corpuscles which feed on the germs as they multiply in the infected tissues. The whole practice of modern surgery is based on absolute cleanliness in the treatment of wounds to prevent the entrance of bacteria during operations.

There are some serious bacterial diseases of plants, as the pear and apple blight, cucumber and melon wilt, black rot of cabbage, wet rot of potatoes, and hyacinth blight, and probably peach yellows is also of this class.

258. Public health. The matter of public health and hygiene calls for constant attention on the part of physicians and health officers to the possible sources of germ diseases. For example, contaminated water and impure milk are the commonest means of infection for typhoid fever, and epidemics of this disease are frequently traced to these sources. We cannot emphasize these points better than by studying the history of a typical typhoid epidemic, taking as our illustration the well-known outbreak in 1885, in Plymouth, Pennsylvania, a town of about eighty-five hundred inhabitants. Typhoid fever appeared in the spring with such violence that from fifty to two hundred cases developed daily, until about eleven hundred persons were stricken (about one eighth of the population), more than one hundred of whom died. The disease appeared only in persons who drank the hydrant water from certain town reservoirs, and those who used private wells escaped. On investigation the following facts were established. During the winter a case of typhoid fever, contracted in Philadelphia, had been cared for in a house which stood close to a stream that flowed into the town reservoirs. During the illness intestinal discharges from the patient had been thrown out upon the snow within a few feet of this stream. During late March and early April the snow melted and there were frequent rains that washed the germ-laden material into the stream, which carried it into the reservoirs. The first cases of typhoid fever in the epidemic appeared within two or three weeks (the period of incubation in typhoid fever) after the infected water had been distributed through the town. Thus the entire epidemic was due to the carelessness or ignorance of attendants who did not safely dispose of the germ-filled wastes from a typhoid patient.

The terrible outbreaks of cholera are usually due to infection of water supplies. The germs of tuberculosis are very widely distributed by means of the dried sputum of diseased persons, hence the importance of rules against spitting in public places. The common diseases incident to the association of children in school, such as diphtheria, scarlet fever, measles, and mumps, make necessary the strict isolation of all cases until there is no possible danger of contagion. As the sources of germ infection are reduced or stamped out, the possibilities of germ diseases become at once lessened. The healthy human body is wonderfully resistant, and the problem of public health is largely the practical one of combating germs. So important are the bacteria in disease and hygiene that a science has developed, called *bacteriology*, with elaborate methods of its own to which specialists give their entire attention.

CLASS VI. THE YEASTS, OR *SACCHAROMYCETES*

259. The yeasts. The yeasts are much larger than the bacteria, and have a more complex cell structure, for there is present a clearly defined nucleus. The cells reproduce in a peculiar manner called *budding*, and the yeasts are frequently termed *budding fungi*. Small extensions are put forth from the cells (Fig. 209, *A*), which, after increasing in size, become cut off from the parent structure. The parent and daughter cells frequently remain attached in short chains or clusters. The relationships of the yeasts are very obscure, but there are reasons for believing them to be degenerate conditions derived from some types of higher fungi whose spores are known at times to pass into yeast-like forms when cultivated in sugary solutions.

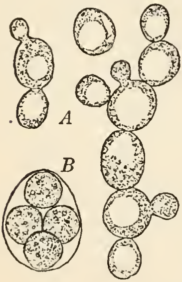

Fig. 209. Yeast (*Saccharomyces cerevisiæ*)

A, vegetative cells, showing method of budding; *B*, spore formation

Yeasts are chiefly interesting as the agents of alcoholic fermentation by which sugar dissolved in water is changed into alcohol and the gas carbon dioxide. The alcoholic nature of wines, beers, ales, and hard cider is due to the fermentation of grape juice, wort, or sweet cider, all of which contain sugar, and the froth and bubbles of gas which escape from the fermenting fluid is carbon dioxide. The yeasts are distributed very widely, and they are sure to be introduced by dust into any sugar solution that is not sealed up. Therefore weak sugar solutions ferment spontaneously if left exposed, although it is the practice in the manufacture of beers and some wines to use special kinds of yeasts that are cultivated for the purpose. The yeasts that are distributed indiscriminately by the air are called *wild yeasts*, to distinguish them from those which are cultivated for the purposes of brewing and bread making. The wild yeasts sometimes become established in cheeses and other dairy products, and also in breweries, where they set up fermentations that render the food or drink unfit for use.

The raising of bread results from the fermentation by yeast of sugar that is present in the dough.[1] The cavities, or holes, in the dough are formed by bubbles of carbon dioxide which, with the small percentage of alcohol developed, is driven off in the baking. Compressed yeast is made in certain distilleries from cultures in large vats, whose yeast scum is removed and pressed into the yeast cakes that are sold for domestic use.

CLASS VII. THE ALGA-LIKE FUNGI, OR *PHYCOMYCETES*

260. The alga-like fungi. The *Phycomycetes* (meaning alga-fungi) comprise a large number of forms which resemble the algæ in their structure and methods of reproduction. Some of them are one-celled and microscopic, but others are very conspicuous mold forms, and certain types are destructive parasites that cause some very serious plant diseases. The interesting fungus (*Empusa*) which kills the house flies, that are frequently found attached by their mouth parts to window panes and woodwork, is in a special group of this assemblage. We shall only be able to consider representatives of the following three orders of this interesting class of the fungi: (1) the molds, (2) the water molds, and (3) the blights and rots.

261. The molds. The molds (order *Mucorales*) form very extensive and conspicuous shining cobweb-like growths (Fig. 210) through and upon the material of manure heaps and other

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[1] See the paper by Helen W. Atwater, "Bread and the Principles of Bread Making," United States Department of Agriculture, *Farmer's Bulletin 112*, 1900.

masses of decaying matter. It is desirable that the term *mold* should be restricted to fungi of this group.

The bread mold (*Rhizopus nigricans*) illustrates well the characters of the group. An extensive growth may always be obtained on bread by placing it in air saturated with moisture, as under a bell jar set in a dish of water. The vegetative body consists of large branched filaments which generally appear glistening white because they are covered with minute drops of moisture. The individual filament of a fungus is called a *hypha* (meaning a web), and a mass of hyphæ is termed a *mycelium*. The hyphæ of the bread mold resemble the filaments of *Vaucheria* (Sec. 228) in having no cross partitions, the filaments being a single chamber from end to end, and consequently a cœnocyte (Sec. 229). The multinucleate protoplasm forms a layer under the wall of the hypha and contains

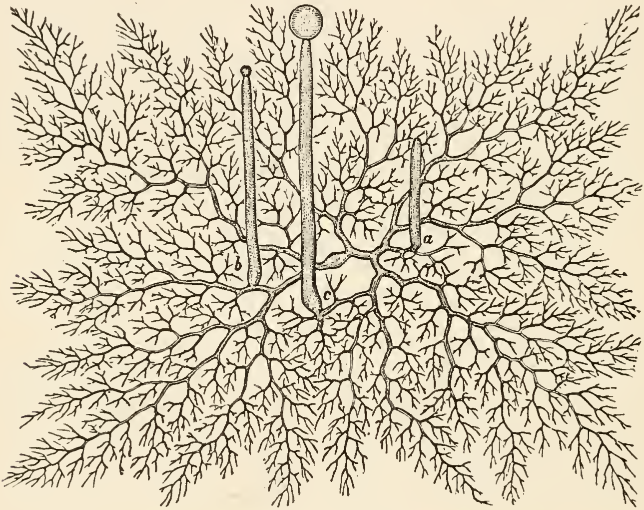

Fig. 210. The mycelium of a mold (*Mucor Mucedo*) developed from a single spore

a, *b*, and *c*, erect branches which are to bear the sporangia, showing three stages of development. — After Brefeld minute globules of a fatty nature. The bread mold is an excellent example of a saprophytic fungus. The hyphæ grow all through the porous substance of the moist bread and absorb fluids containing products of the bread's incipient decay. The material over which a saprophytic fungus grows and upon which it lives is called its *substratum.*

The fructifications of the bread mold are very characteristic. Numerous erect branches arise, several in a group, from creeping hyphæ that develop clusters of short, root-like filaments at these points (Fig. 211). The end of each erect branch then gradually enlarges and becomes separated from the stalk below by a dome-shaped cross wall called the *columella* (Fig. 212, *A*). The terminal cell becomes a spore case, or sporangium, and develops a multitude of smoke-colored spores, which make the spore cases appear as black heads upon the upright stalks (Fig. 212, *B*). The spores are distributed by the breaking of the sporangium wall, exposing the dome-shaped columella which remains at the end of the stalks after the dispersal of the spores (Fig. 212, *D*).

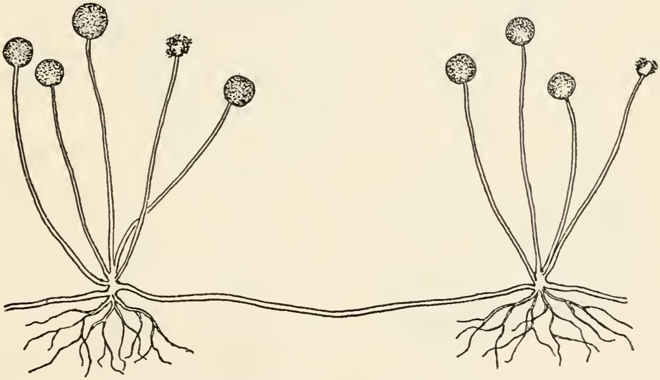

Fig. 211. Growth habit of the bread mold (*Rhizopus nigricans*)

Sketch showing two groups of erect hyphæ bearing sporangia, with root-like clusters of filaments at their bases

The molds have a remarkable method of sexual reproduction, which is, however, rarely found in the bread mold (*Rhizopus*), but is not uncommon in other genera, as *Mucor* and *Sporodinia.* Two short branches from the mycelium become applied to one another, end to end (Fig. 213, *A*). The tip of each then becomes cut off as a sexual cell, or gamete (Fig. 213, *B, C*), peculiar in having very many nuclei, and consequently called a *cœnogamete.* The two gametes finally fuse, and a large zygospore (Fig. 213, *D*) with heavy black walls is formed between the filaments. It is probable that the sexual nuclei from the two gametes fuse in pairs within the zygospore.

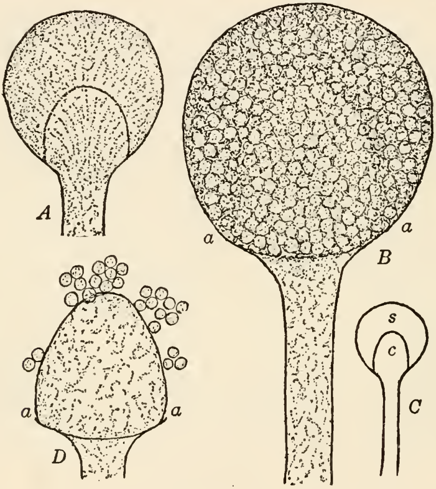

Fig. 212. The sporangium of the bread mold (*Rhizopus nigricans*)

A, young sporangium, showing dome-shaped cross wall (columella) shortly after its formation; *B*, mature sporangium, the columella being hidden by the spores; *C*, diagram of a lengthwise section of a sporangium; *s*, spore cavity; *c*, columella. *D*, columella after the rupturing of the sporangium wall, which was attached along the line *a* corresponding to similar line in *B*; clusters of spores still clinging to the columella

262. The water molds. The water molds (order *Saprolegniales*) are very remarkable aquatic fungi which grow on the dead bodies of insects when immersed in pond or ditch water (Fig. 214, *A*). Certain species attack the gills and mouths of young fishes in hatcheries and may be very destructive. The cœnocytic hyphæ live in the tissues of the animal, and filaments grow out from them freely into the water, where they develop the reproductive organs.

Zoöspores are formed numerously in terminal club-shaped sporangia and are discharged into the water (Fig. 214, *C*, *D*). They are two-ciliate and constitute the method of rapid multiplication, swimming about in the water, seeking a favorable substratum on which to settle down.

The sexual organs are male and female. Globular oögonia are formed at the ends of certain hyphæ, and each develops a number of eggs (Fig. 214, *F*). The male organs are delicate antheridial filaments which arise below the oögonia or from neighboring hyphæ. These apply themselves to the oögonia and send delicate tubes (conjugation tubes) into the interior, which in some forms are said to unite with the eggs. However, it is known that the antheridial filaments in many of the water molds perform no function, and indeed are not even present in some types. In such cases the eggs mature into oöspores without fertilization. The water molds furnish, then, excellent illustrations of the degeneration of a sexual process, a phenomenon found in other groups of fungi.

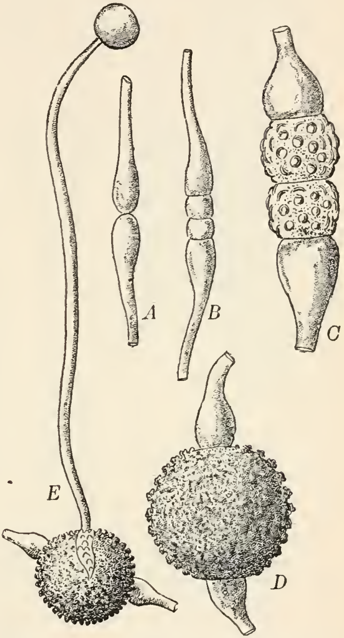

Fig. 213. Formation of zygospores in a mold (*Mucor Mucedo*)

A, two hyphæ in contact, end to end; *B*, the terminal gametes; *C*, later stage, the gametes fusing; *D*, a ripe zygospore; *E*, germination of a zygospore, the filament forming a sporangium at once in this case.— After Brefeld

The suppression of a sexual act is termed by botanists *apogamy* (meaning without marriage), or sometimes *parthenogenesis*, when the egg itself develops without fertilization. Apogamy is found in many groups of plants,— in the algæ and fungi, among the ferns, and even in the seed plants.

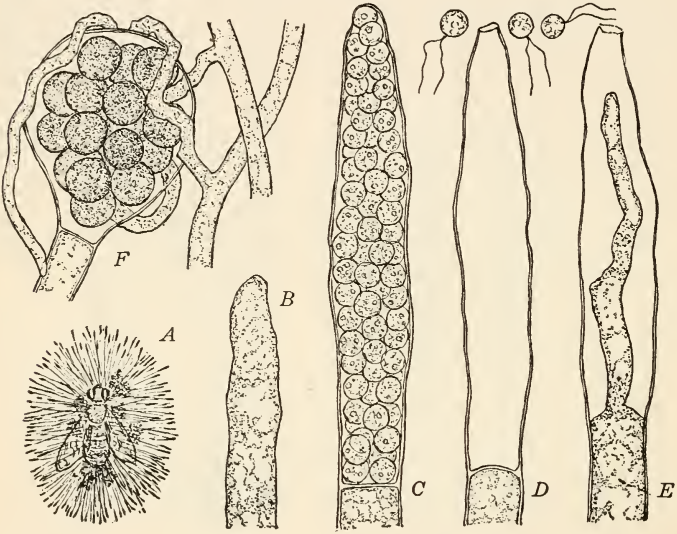

Fig. 214. A water mold (*Saprolegnia mixta*)

A, habit sketch of the mycelium around a fly; sporangia being formed at the tips of the longest hyphæ and sexual organs nearer the body of the insect; *B*, tip of hypha; *C*, terminal sporangium filled with zoöspores; *D*, empty sporangium with a group of zoöspores near the opening; *E*, empty sporangium with the hypha continuing its growth inside; *F*, an oögonium containing many eggs and with three antheridial filaments applied to it

263. The blights. The blights (order *Peronosporales*) are parasitic fungi which cause some very destructive plant diseases. Some of them are also called "downy mildews," but it would be better if the term *mildew* were reserved for a peculiar group of sac fungi (Sec. 266). The hyphæ form extensive growths in the tissues of the hosts. The asexual fructifications appear on the surface, but the sexually formed oöspores are developed within the host. The type most available for study is the blister blight (*Albugo*), but the potato blight, or rot, and the grapevine blight (downy mildew) are, for economic reasons, the most important forms in the group.

Fig. 215

The blister blight (*Albugo candida*)

Blisters containing conidia on the stem of the shepherd's purse (*Capsella*)

The blister blight. The blister blight (*Albugo*) grows on the shepherd's purse (*Capsella*) and not infrequently on the radish, appearing as white blisters on the leaves and stems (Fig. 215). The blisters are formed by the asexual fructifications, which consist of masses of spores called *conidia* that are developed in chains from the ends of hyphæ just underneath the epidermis (Fig. 216, *A*, *B*). Conidia are air spores of fungi, — that is, spores formed singly or in chains at the ends of special branches and scattered in the air. Those of *Albugo* are distributed by the wind after the breaking of the blisters, and germinate in moisture, developing

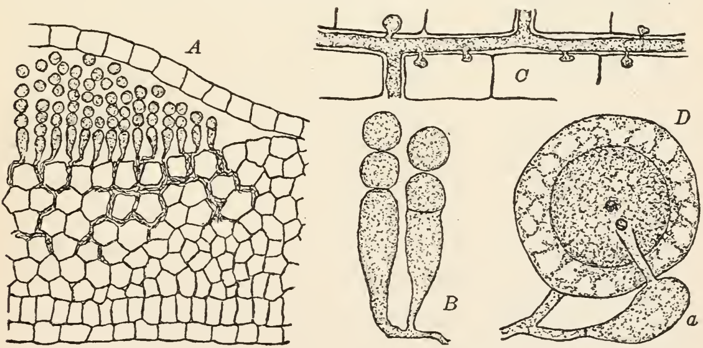

Fig. 216. Reproductive organs of the blister blight (*Albugo candida*)

A, section through the edge of a blister on a leaf; the air spores, or conidia, are formed in chains under the epidermis from the swollen tips of fungal filaments growing between the cells of the leaf; *B*, tips of two filaments, showing development of the conidia serially; *C*, a filament showing sucker-like structures (haustoria) which enter the cells of the host; *D*, the sexual organs; the male cell, or antheridium, *a*, has just discharged its nucleus through a beak-like process into the single egg within the oögonium several two-ciliate zoöspores. If the conidium has germinated on the proper host after a rain or heavy dew, the zoöspores swim over the moist surface, and finally coming to rest they put forth delicate germ tubes that enter the host through one of the breathing pores or stomata. The sexual organs are generally found in portions of the leaves and stems which become much swollen and colored reddish or purplish. The large oögonium forms a single egg and is accompanied by a single antheridial filament which develops from the hypha below (Fig. 216, *D*). The antheridial filament puts forth a tube-like process which enters the oögonium and discharges one or more nuclei into the egg, fertilizing it. The fertilized egg develops heavy walls, becoming an oöspore, which rests during the winter, and on germinating in the spring produces a large number of zoöspores that infect new hosts.

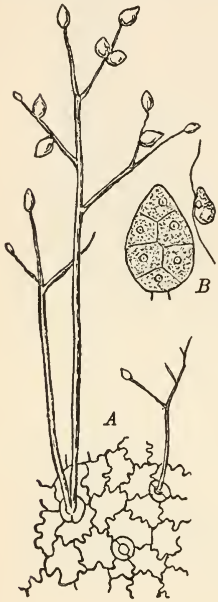

FIG. 217. Conidial fructification of the potato blight (*Phytophthora infestans*)

A, the air spores (conidia) formed on long filaments which grow out from the interior of the potato leaf through the stomata; *B*, the development of zoöspores in a conidium; a single zoöspore is shown at the right. — After Schenck

The potato blight, or rot. The potato blight (*Phytophthora infestans*) has a different type of conidial fructification from *Albugo*. The hyphæ emerge from the leaves through the stomata (Fig. 217, *A*), and conidia are formed freely in the air in immense quantities. These air spores are distributed by the wind, and germinating in moisture develop zoöspores (Fig. 217, *B*), which infect new hosts, as in *Albugo*. Cloudy, wet, and windy seasons are naturally especially favorable to the spread of the potato blight. The green parts of a blighted potato plant wither, and the potatoes either cannot be formed, or rot in the ground. The disease is carried over from one year to the next in diseased potatoes that are planted. The potato blight came originally from South America (perhaps Peru) and first appeared in Europe in 1845, probably introduced from North America. The disease spread very rapidly, causing local famines in various countries, notably in Ireland. It is now, however, largely held in check by spraying the plants with Bordeaux mixture, which contains copper and is poisonous to the fungus.

The grapevine blight, or downy mildew. This genus (*Plasmopara*) develops conidia on hyphæ outside of the host plant, as in the potato blight, but they germinate by tubes instead of forming zoöspores. The disease had its origin in America, but our vines are not generally very seriously injured by it. However, when it was accidentally introduced into Europe it proved a terrible menace to the vine-growing industries there. The European varieties of grapes are largely grafted upon American rootstocks because the latter resist the attacks of a very destructive insect pest called *Phylloxera*. But the American grapevine blight was for a time more injurious than the insect, until means were discovered of keeping it in check by spraying the vines with Bordeaux mixture.

The interesting genus *Pythium*, which causes the "damping off" of seedlings, and is sometimes very destructive in greenhouses, is related to the blights.

264. Summary of the alga-like fungi. The chief points of resemblance of the *Phycomycetes* to certain algæ lie in the cœnocytic structure of the fungal filaments and the development of zoöspores in terminal sporangia. The sexual organs are likewise similar to those of algæ in that they are developed terminally, but there are important modifications because motile sperms are not generally formed. However, motile sperms are known for one type (*Monoblepharis*). The conidia are plainly modified sporangia, which become detached from the parent filaments and are distributed as special reproductive spores. The algæ which most resemble the larger filamentous *Phycomycetes* are such forms as *Vaucheria* (Sec. 228), and other types of the *Siphonales*, and some authors believe that the molds, water molds, and blights have been derived from that general region of the algæ.

CLASS VIII. THE SAC FUNGI, OR *ASCOMYCETES*

265. The sac fungi. The sac fungi are distinguished by a peculiar type of reproduction, through spores which are developed, generally eight in number, in a special unicellular organ called an *ascus* (plural, *asci*), which means a sac. The asci are produced sometimes in very great numbers in a fructification termed an *ascocarp*, or sac fruit, which is a structure of importance. The filaments, or hyphæ, of the sac fungi are divided by cross walls into cells, and are never long cœnocytes, as in the alga-like fungi (*Phycomycetes*). The *Ascomycetes* is one of the two largest groups of the fungi, comprising more than fifteen thousand species. We can only describe a few forms from the following groups: (1) the mildews, (2) the cup fungi, and (3) the knot and wart fungi.

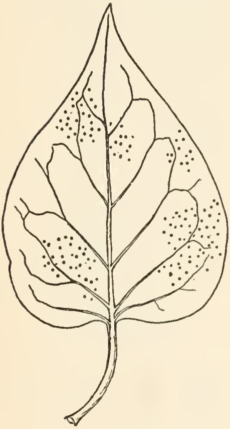

FIG. 218. Sac fruits (ascocarps) of the lilac mildew (*Microsphæra Alni*) on the lower surface of a lilac leaf

266. The mildews. The true mildews (order *Perisporiales*) are a very clearly defined group of fungi, and it is desirable that the term *mildew* be restricted to them. They are mostly external parasites, very common on the leaves of many seed plants, such as wheat, lilac, Virginia creeper, grapes, verbena, cherry, oak, willow, etc. The hyphæ form a cobweb-like growth (mycelium) over the leaves, and put forth sucker-like processes called *haustoria*, which enter the epidermal cells of the host. There is a method of rapid multiplication during the summer months by air spores, or conidia, which are formed in chains from the ends of erect hyphæ (Fig. 219, *A*) and give the leaves a powdery appearance. But the most important fructifications are the sac fruits (ascocarps), which appear later in the season as black dots on the leaves. They can be most conveniently studied in the lilac mildew.

The lilac mildew. This type (*Microsphæra Alni*) forms white blotches on the leaves of the lilac, especially over somewhat

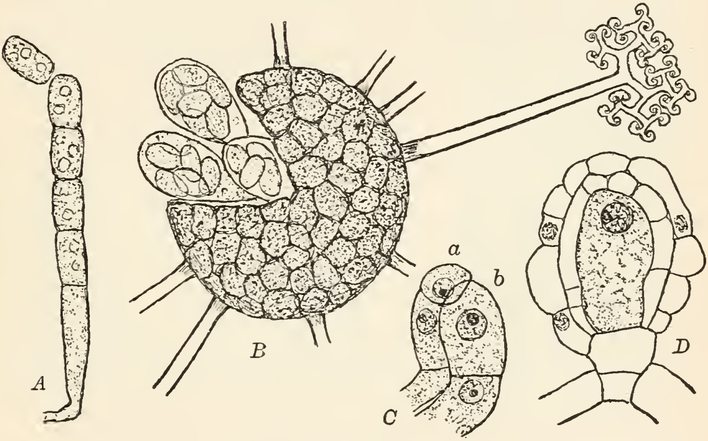

Fig. 219. Reproductive organs of the mildews

A, *B*, the lilac mildew (*Microsphæra Alni*): *A*, a chain of air spores (conidia) formed from the tip of an erect filament; *B*, a sac fruit (ascocarp) cracked open, with two spore sacs (asci) protruding, one of the appendages shown in detail. *C*, *D* (*Podosphæra*): *C*, the sexual organs, — *a* the antheridium, *b* the female gamete or ascogonium; *D*, the development of the cellular envelope of the sac fruit around the fertilized female gamete. — *C*, *D*, after Harper

shaded portions of the plant. The sac fruits are found in the autumn as black globular bodies made up of filaments so closely united that they form a cellular mass (Fig. 219, *B*), in the interior of which are developed the spore sacs (asci). The sac fruit of *Microsphæra* has several radiating appendages with peculiar tips. It is developed as the result of a sexual process involving the fusion of two sexual cells, or gametes (Fig. 219, *C*). The asci are formed at the ends of hyphæ that arise from the fertilized female cell, while the wall of the ascocarp is formed from neighboring filaments (Fig. 219, *D*). The ascocarp thus resembles in its development the sexually formed fructification (cystocarp) of certain red algæ such as *Polysiphonia* (Sec. 245). The ascocarp, like the cystocarp, is a system of two tissues, one derived from the fertilized female gamete (called an *ascogonium*) and the other from the vegetative cells of the parent plant. The phase in the life history beginning with the fertilized ascogonium and ending with the production of ascospores is an asexual or sporophyte generation alternating with the sexual generation or gametophyte, as in the red algæ (Sec. 246). The wall of the sac fruit is clearly a protective structure for the sacs, each of which generally develops six spores in the lilac mildew, although eight nuclei are present in the sac.

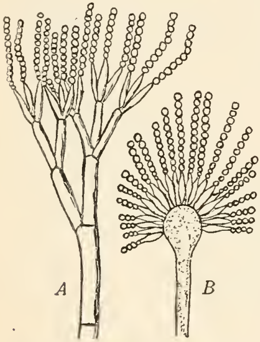

Fig. 220. Green and yellow mildews

A, the green mildew (*Penicillium*); *B*, the yellow mildew (*Aspergillus*)

The green and yellow mildews. These are very common saprophytes on bread, cheese, shoes, clothing, and other substances that mildew or "mold" in dampness. They are easily distinguished by their colors and the structure of the conidial fructifications. The green mildew is *Penicillium* (Fig. 220, *A*), which is believed to give the peculiar flavor to Roquefort cheese. The yellow mildew is *Aspergillus* (Fig. 220, *B*). Their ascocarps are rather uncommon, especially those of *Penicillium*.

267. The cup fungi. Most of the conspicuous forms in this very large assemblage belong to the order *Pezizales*. The sac fruits are saucer-, cup-, or funnel-shaped (Fig. 221, *A*, *B*), frequently colored yellow, orange, red, brown, or bluish, and in some forms are three or more inches in diameter. The cup fungi are almost all saprophytes, and are found on rotten logs and earth in damp woods, forming very striking and beautiful growths. The chief peculiarity of the ascocarps is the fact that the entire inner surface of the cup is a fruiting surface, consisting of immense numbers of asci, arranged upright and all parallel with one another, among delicate sterile filaments (Fig. 221, *C*). The asci are thus exposed, imbedded in a fruiting surface, and are not inclosed in a case, as in the mildews.

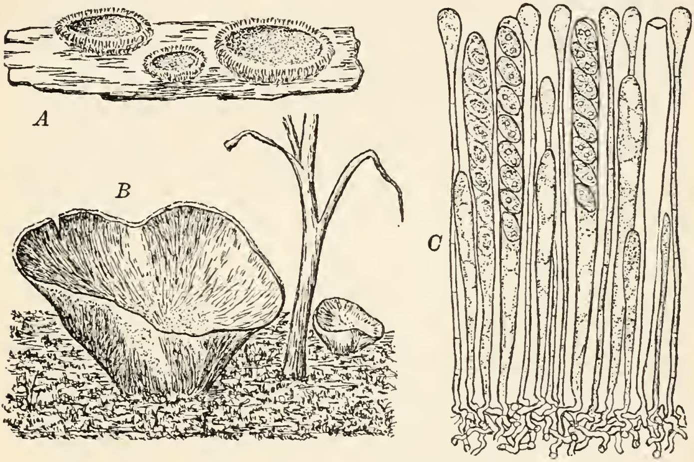

Fig. 221. Cup fungi

A, *Lachnea*, a small hairy form frequently growing on wood; *B*, *Peziza*, a large form growing on earth; *C*, section through the fruiting surface of a *Peziza* type, showing asci in various stages of development among delicate sterile filaments (paraphyses)

The sac fruits of some cup fungi (notably *Pyronema*) are known to be developed as the result of a sexual process, but there is probably a great deal of sexual degeneration in this group of the fungi, as in the water molds (Sec. 262).

The morel. Some very striking large forms are closely related to the cup fungi. Among them is the morel (*Morchella*), much prized as one of the best of the edible fungi (Fig. 222), and some other curiously shaped types (*Helvella, Mitrula, Geoglossum*, etc.).

Fig. 222. The morel (*Morchella*), an edible sac fungus

The convoluted upper portion is an exposed fruiting surface

The fruiting surface of the ascocarps is sometimes very extensive, and is thrown up into irregular lobes and ridges.

268. The knot and wart fungi. This large group contains forms with peculiar hard black or brown wart and scab-like fructifications, which are found on the bark of trees. Most of the species are saprophytic, but some, as the black knot (Fig. 223), on the plum and cherry, are very destructive parasites. The outer parts of the sac fruits contain immense numbers of small cavities (*perithecia*) that are lined with asci. Very little is known of the development of such complex sac fruits, but it is probable that many of these fungi are sexually degenerate, as are some of the cup fungi. *Xylaria*, with its large finger-like fructifications, belongs to this group.

Fig. 223. The black knot (*Plowrightia*) on a branch of the cherry

The branches become distorted, and long cracks are formed, greatly impairing the strength of the trees

269. Other sac fungi. Several exceptional sac fungi deserve special mention.

Ergot. Ergot grains (Fig. 224, *A*) are hard black structures found in heads of barley, rye, wheat, and certain grasses, notably the wild rice. They are really the mummified and distorted ovaries, or grains whose tissues have become filled and destroyed by the mycelium of the fungus (*Claviceps*). The ergot represents a sort of resting stage in the life history of the fungus, and from it are developed in the spring purplish stalks bearing the sac fruits (Fig. 224, *B*).

The caterpillar and grub fungi. These extraordinary parasites (*Cordyceps*) grow in the bodies of certain caterpillars and other larvæ, and in their pupæ. The body cavity of the insect becomes filled with the mycelium, and generally mummified, after which a long-stalked sac fruit grows out from between certain segments (Fig. 225).

FIG. 224. The ergot (*Claviceps*)

A, ergot grains on a head of barley; *B*, small sac fruits (ascocarps) developing from an ergot grain. — *B*, after Tulasne

The truffles. The truffles are very remarkable sac fruits, sometimes as large as potatoes, which are developed on mycelium that is generally associated with the roots of certain trees. The commonest truffle on the market (*Tuber brumale*) comes from the region of Perigord, in central France, and is the most prized of all the edible fungi. It grows under certain kinds of oak trees, and is found by dogs and swine that are trained to discover its location, and which detect the fungus by a characteristic odor. The association of the mycelium of the truffle with the roots of the oak tree is an excellent example of what is called a mycorrhiza, and is discussed in Sec. 278.

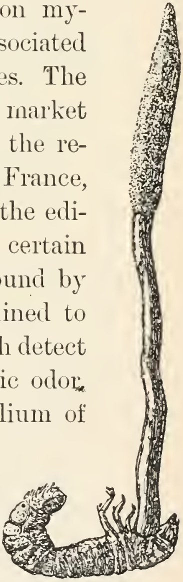

FIG. 225

Caterpillar fungus (*Cordyceps*) growing out of the larva of the May beetle, which lives underground

The spot fungi and rots. The spot diseases of plants are numerous, and mostly upon the leaves and fruit. Many of them are caused by sac fungi, as the strawberry-leaf spot (*Sphærella*), black spots on grasses and clover (*Phyllachora*) resembling rust spots, tar spots on willow and maple (*Rhytisma*), and the apple scab (*Venturia*). Some of the most destructive rots are sac fungi, though frequently caused by some kind of conidial fructification rather than by the sac fruit. Among them are the bitter rot of apples (*Glomerella*), brown rot of peaches and plums (*Sclerotinia*), and plum pockets (*Exoascus*).

270. The imperfect fungi. Some other spot diseases and rots are caused by fungi which are known only through conidial or other types of asexual fructification. More species of these forms have been described than of all the sac fungi together, and they are assembled in a group called the *Fungi imperfecti.* Some of them are very important economically, causing such diseases as the potato scab (*Oöspora*), tar spots (*anthracnose*) on beans (*Colletotrichum*), black rot of tomato (*Macrosporium*), and black rot of apples (*Sphæropsis*). Most of the *imperfect fungi,* however, are saprophytes, and play an important part with other saprophytic fungi in bringing about the decay of vegetable débris.

271. The lichens. The lichens deserve special consideration as a very remarkable group. They are not single plants, but composite organisms made up of algæ which are contained in an enveloping mesh of fungal filaments. The algal cells showing through the fungal layers frequently give the lichen a greenish color, but other pigments may be present, and some lichens have brilliant yellow, orange, brownish, and reddish tints. Lichens have a great variety of forms. Some grow closely pressed against rocks and tree trunks (*crustaceous,* Plate V, *A*), some are leaf-like (*foliose,* Fig. 226), and some are much branched (*fruticose,* Fig. 227).

The fructification of a lichen is most commonly a saucer- or cup-shaped structure. The inner surface is a fruiting layer (Plate V, *B*), and contains numerous eight-spored sacs, or asci (Plate V, *D*), showing clearly that the fungi concerned in the lichen are sac fungi, or *Ascomycetes.* The fructifications are therefore sac fruits, or ascocarps, and these are known in some forms to develop as the result of a sexual process. Most of the

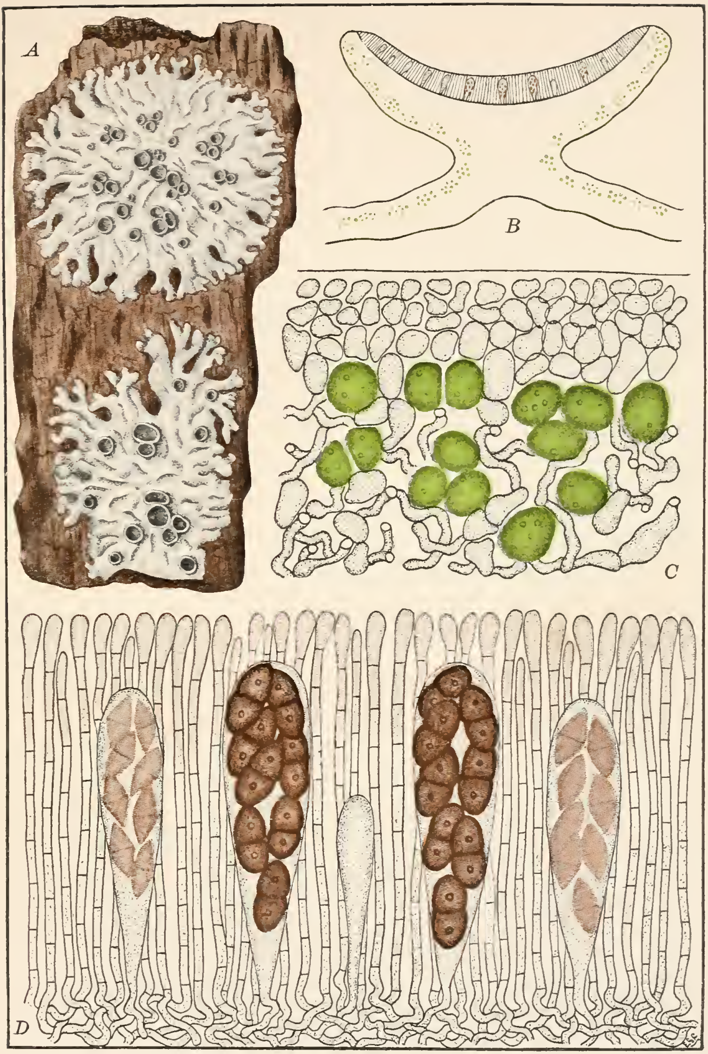

Plate V. A Common Tree Lichen (*Physcia stellaris*)

A, habit sketch; *B*, diagram of a section through a sac fruit (ascocarp), showing the fruiting surface and layer of algal cells; *C*, section showing a group of algal cells (*Pleurococcus*), held in the network of fungal filaments; *D*, section of the fruiting surface, showing sacs (asci) in stages of development among the sterile filaments (paraphyses)

lichens have sac fruits closely resembling those of the cup fungi. There is one small group of tropical lichens whose fungal portions are basidia fungi, or *Basidiomycetes,* and not *Ascomycetes.*

The algal portions of a lichen may be scattered, but in some types they are arranged in definite layers. The kinds of algæ differ in various lichens. Some of them are unicellular green forms, evidently of the genus *Pleurococcus* (Plate V, *C*). Most of the species belong to the blue-green algæ, one-celled forms being commonest, though some complicated filamentous types, such as *Nostoc,* are found in certain lichens. One curious lichen, which grows on the leaves of the coffee plant, contains a species of *Coleochæte* (Sec. 222).

The development of the present clear understanding of the composite, or fungal and algal, nature of lichens makes one of the most interesting chapters in the history of botanical science. First came the recognition of the colorless portion of the lichen as fungal and the colored elements as algal in character. Then these portions were separated and cultivated independently of one another, which proved that they remained respectively algæ and fungi; for example, the lichen spore never developed into algal cells, but only into fungal filaments. Finally, lichens were created by bringing germinating spores in contact with wild algæ of a suitable kind, and these lichens have in some cases lived for many months, finally developing typical lichen sac fruits (ascocarps), thus completing the life history.

The lichens are perhaps chiefly interesting for the relations which the algæ and fungi bear to one another. When two organisms live in intimate physiological association, so that both receive some benefit from the partnership, the condition is called *symbiosis* (meaning a living together). The mycorrhiza relationship (Sec. 278) is an excellent illustration of symbiosis. It is not easy to analyze critically the relationships between the algæ and fungi in a lichen association, but some points seem clear.

First. The fungi are absolutely dependent upon the algæ for their organic food (such as the carbohydrates), which, of course, the algæ are able to manufacture in the manner characteristic of green plants (photosynthesis). The relation of the fungus to the alga is then in all essentials that of a parasite to its host.

FIG. 226. A leaf-like, or foliose, lichen (*Cetraria*). *s*, sac fruits

Second. The algæ receive a certain sort of protection in the lichen thallus. Thus they have fixed positions on exposed rocks, cliffs, trees, and other objects where they could hardly grow otherwise, or at least not in the same luxuriance. The substance of the lichen also retains moisture, so that the algal cells are not so subject to drought.

It is well known that many of the lowly algæ would grow in situations frequented by lichens if left alone, and it is evident that the lichens arise because fungus spores fall among the algæ, and germinating produce hyphæ which live parasitically upon them as hosts. The algæ are then, in a sense, slaves of the fungi. They are not killed, for that would be of no advantage to the fungus, which requires them to manufacture its organic foods. The term *slavery* perhaps best expresses the relation of the algæ to the fungi in the lichens.

Life habits of the lichens. Lichens are found on rocks, cliffs, branches and trunks of trees, and on the ground, when the latter cannot support green vegetation, either because it is too barren, or is exposed to unfavorable climatic conditions. They are most luxuriant in temperate and sub-arctic regions, especially where there is much rain. They form the bulk of the vegetation on the tops of mountains and in the arctics, where grass and other alpine seed plants cannot grow. They are abundant along storm-swept seacoasts. Some forms actually cover large areas, as the reindeer moss (*Cladonia rangiferina*, Fig. 227, *A*), which in extreme northern countries furnishes an important source of food for herbivorous animals, as the reindeer. Since the lichens are the first plants to grow on exposed rocks, they form there the first soil, mingled with decayed vegetable matter (*humus*), which may furnish a foothold for higher plants, such as the mosses and grasses, that are constantly trying to establish themselves in the territory of the lichens.

Some uses of lichens. Some lichens (*Roccella*) yield beautiful purple, blue, and crimson dyes called orchil and cudbear, much used in former centuries in Italy, and later in other parts of Europe. Orchil when prepared with soda or potash yields the dye litmus, employed in the manufacture of litmus paper. Other lichens, as Iceland moss (*Cetraria*), are ground up and mixed with wheat and made into cakes.

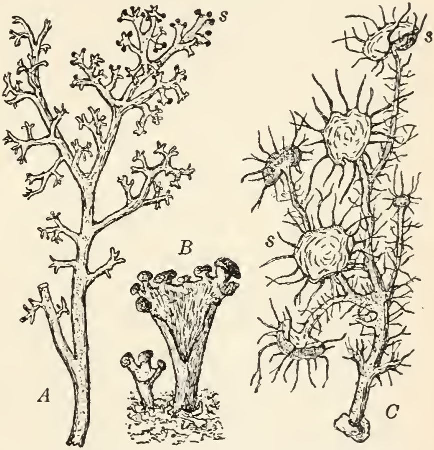

Fig. 227. Some branching, or fruticose, lichens

A, the reindeer moss (*Cladonia rangiferina*); *B*, *Cladonia cornucopioides*; *C*, *Usnea barbata*; *s*, sac fruits

272. Summary of the sac fungi. The most remarkable feature of the life history of the *Ascomycetes* is the position of the ascocarp as a sporophytic phase following the sexual process and alternating with sexual plants, or gametophytes. The ascocarp holds a place in the life history similar to that of the cystocarp in the red algæ (Sec. 246). There are numerous types of asexual spores (such as conidia) in the *Ascomycetes*, which cannot be described here but greatly complicate the classification of the forms. Some authors believe that the sac fungi hold relations to the red algæ, and, indeed, have been derived from them.

CLASS IX. THE BASIDIA FUNGI, OR *BASIDIOMYCETES*

273. The basidia fungi. The *Basidiomycetes* come next to the *Ascomycetes* in number of known species, which is about fourteen thousand. The group takes its name from a peculiar type of reproductive organ called a *basidium* (meaning a small pedestal). The basidium (Fig. 238) is a somewhat swollen terminal cell of a filament, or hypha, from which are developed a group of four spores on delicate stalks called *sterigmata*. The hyphæ of the basidia fungi are divided into cells, as in the sac fungi.

The basidium is a very characteristic structure of the higher forms of the *Basidiomycetes*. However, there are some types, as the smuts and rusts, in which the basidium is represented by a peculiar phase in the life history (the *promycelium*), which does not at first thought seem to resemble the basidium. These points can only be made clear after a study of representative types, and they will be referred to later in the summary of the basidia fungi (Sec. 279). This peculiarity is the basis of a classification of the basidia fungi into two series: (1) the *Protobasidiomycetes*, which are preliminary to (2) the *Eubasidiomycetes*, or typical basidia fungi. The representatives that can be considered here will accordingly be grouped as follows:

Series I. The simpler basidia fungi, or *Protobasidiomycetes*.
   1. The smuts, or *Ustilaginales*.
   2. The rusts, or *Uredinales*.

Series II. The typical basidia fungi, or *Eubasidiomycetes*.
   3. The coral fungi, the pore fungi, the tooth fungi, the gill fungi, collectively called *Hymenomycetes*, and divided into several orders.
   4. The puffballs, the earth stars, the nest fungi, the carrion fungi, collectively called *Gastromycetes*, and divided into several orders.

SERIES I. THE SIMPLER BASIDIA FUNGI, OR *PROTOBASIDIOMYCETES*

274. The smuts. The smuts (order *Ustilaginales*) are parasites which have the peculiar habit of attacking the floral parts, and especially the ovaries, of various members of the grass family. The hyphæ fill these parts with a dense mycelium, destroying the tissue of the host. Finally, most of the cells in the mycelium take on heavy walls and become resting cells, or winter spores, which form the black powdery mass so characteristic of the smut fructification. These resting cells survive the winter and germinate in the spring. Each cell then puts forth a short filament called the *promycelium* (Fig. 228, *A*), upon which are developed a number of small spring spores called *sporidia*, and these in some cases germinate upon the sprouting host plants, as in oats, putting forth filaments that enter the host and develop a mycelium within, which may not be noticed until the fructifications appear in the floral organs. It is important to note that the sporidia multiply rapidly by budding (Fig. 228, *B*), especially under favorable conditions, as in heavily manured soils, and these buds, or conidia, will infect like the sporidia. These habits of budding led to the theory that the yeasts have been derived from the smuts.

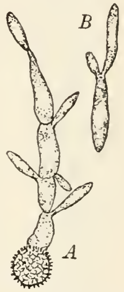

FIG. 228. Promycelium of the corn smut (*Ustilago Maydis*)

A, with spring spores (sporidia) attached; *B*, spring spores budding like yeast cells. — After Brefeld

Various smuts. The corn smut is, perhaps, the most conspicuous form and very destructive. The infection in the corn is local; that is, the spore masses are formed close to the point of entrance of the fungus. Any tender growing region is subject to infection. The corn smut can only be held in check by burning the spore masses as soon as discovered and by avoiding the use of manure, which gives favorable nutrition for the germination of the spores. The smuts of oats and wheat often cause enormous loss in these crops. The best preventive measures seem to be, treatment of the grains with solutions of copper sulphate, or formalin, or steeping them in hot water for a short time before planting, which kills the smut spores without injuring the grain.[1]

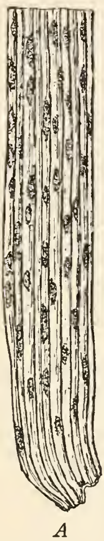

Fig. 229. The wheat rust (*Puccinia graminis*)

A, spots of the red rust on a wheat leaf, composed of the summer spores (uredospores); *B*, spots of the black rust on wheat straw, composed of the winter spores (teleutospores)

275. The rusts. The rusts (order *Uredinales*) cause some of the most disastrous diseases of such grains as wheat, oats, barley, and rye. They are all parasites, forming yellow or black spots on

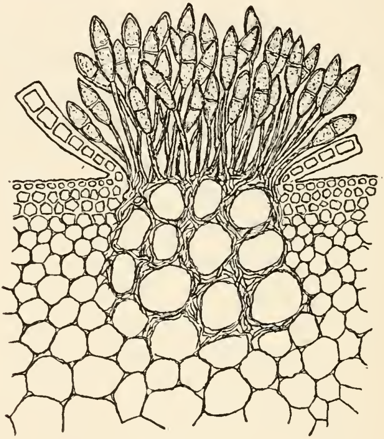

Fig. 230. The winter spores (teleutospores) of the wheat rust (*Puccinia graminis*)

Section through a spot of the black rust on oats, the epidermis of the leaf being thrown back and the two-celled teleutospores raised above the surface on stalks; note the web of fungal filaments (hyphæ) around the very much enlarged (hypertrophied) cells of the host under the spot

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[1] See Swingle, "The Prevention of Stinking Smut of Wheat and Loose Smut of Oats," United States Department of Agriculture, *Farmer's Bulletin 250*, 1906.

the leaves and stems of their hosts. The most complicated life histories in the fungi are found in this group, for many species require two different hosts to complete their life cycle and form a number of different reproductive spores during their development. These peculiarities are best illustrated by the rust of wheat.

The wheat rust. The wheat rust (*Puccinia graminis*) appears on wheat, oats, and other grains and grasses, first as red or yellow streaks or spots upon the leaves and stems (Fig. 229, *A*). The host is greatly weakened and consequently matures only a small yield of grain. Towards the end of the season black streaks (Fig. 229, *B*) are formed in addition to the red-rust spots, and these indicate the development of resting cells, or winter spores, which are peculiar two-celled structures in *Puccinia* (Fig. 230). The winter spores, called *teleutospores,* germinate in the spring, and each cell gives rise to a short filament, the promycelium, usually consisting of four cells (Fig. 231), from which are generally developed four spring spores, or sporidia. The winter spores, promycelium, and spring spores probably correspond to the same stages in the life history of a smut.

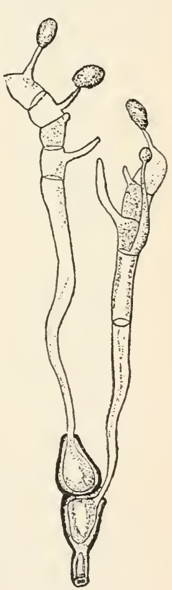

FIG. 231. Promycelium of the wheat rust (*Puccinia graminis*)

After Tulasne

Wherever the barberry is common, as in Europe and New England, the spring spores (sporidia) infect these plants and produce on their leaves peculiar fructifications called cluster cups, or *æcidia* (Fig. 232, *A*, *B*), in which are developed chains of cluster-cup spores, or *æcidiospores* (Fig. 232, *C*). There is considerable evidence to prove that the cluster cups represent the remains of what was once a sexual phase in the life history of the rust, but which is now much modified, and indeed entirely suppressed in some forms.

Curious structures called *spermogonia* (Fig. 232, *C*) frequently accompany the cluster cups and are believed to be the remains of male sexual organs now no longer functional. They develop immense numbers of minute cells, termed *spermatia*, which may at one time have been functional sperms, but apparently serve no useful purpose now.

The æcidiospores are distributed by the wind and germinate upon young wheat, putting forth tubes which enter the host through the stomata. The infected wheat then develops a number of crops of one-celled summer spores called *uredospores* (Fig. 233). The first crops of summer spores are widely scattered in high winds and infect more wheat, thus spreading the disease very rapidly. The spots of uredospores are reddish or yellowish, and this is the stage known as the red rust of wheat. Finally, at the end of the season, the black spots of teleutospores appear, and the rust's life history is completed.

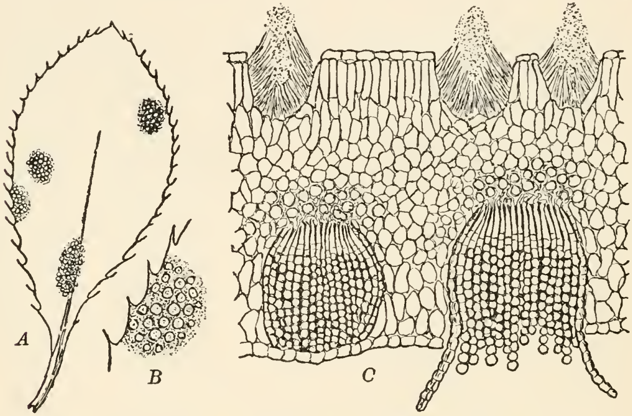

Fig. 232. Cluster cups (æcidia) on barberry leaves

A, habit sketch showing groups of cluster cups on a leaf; *B*, a group enlarged; *C*, section through a leaf showing cluster cups on the lower surface, with the chains of æcidiospores and the male organs (spermogonia) on the upper surface. The latter develop immense numbers of minute cells which probably represent sperms, but are now functionless

This long life history, which is thoroughly known in Europe, becomes much shortened in the Middle West, California, and Australia, where there is no barberry, by the omission from it of that host. In these regions the uredospores (summer spores) may survive the winter or dry season, or be carried over from summer to summer through the winter wheat and germinate directly upon the new developing wheat of the following year, so that the reproduction of the rust is by a succession of the uredospores.

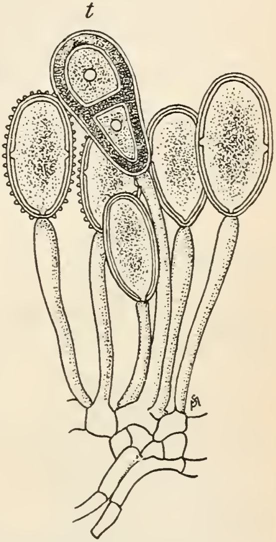

Fig. 233. The summer spores (uredospores) from the red rust of wheat

A single two-celled teleutospore, *t*, happens to be present among them. — After De Bary

There is no method known of killing the wheat rust on the living host; but it has been found that certain varieties of wheat, as the macaroni wheats, are far more resistant to the rust than others. There is some hope that varieties may be bred by crossing our wheats with macaroni wheat that will be largely immune to this disease, which annually causes losses of many million dollars in the United States alone.[1] There are a large number of varieties of *Puccinia graminis*, and also several other species of *Puccinia* which attack various grains, grasses, and other plants. One of these (*P. asparagi*) sometimes causes great damage to asparagus.

Other rusts. The group of the rusts is very large, the genera being distinguished chiefly by the structure of the teleutospores

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[1] For a discussion of the rusts and rust problems of the United States, see papers of Carleton from the publications of the United States Department of Agriculture, "Cereal Rusts of the United States," Division of Vegetable Physiology and Pathology, *Bulletin 16*, 1899; "Macaroni Wheats," Bureau of Plant Industry, *Bulletin 3*, 1901; "Investigations of Rust," Bureau of Plant Industry, *Bulletin 63*, 1904.

and the different types of life histories affecting various hosts; but many of the forms have no economic importance, being found on such plants as the violet, May apple, cocklebur, asters, golden-rods, members of the pea family, etc. However, there are destructive rusts on the roses (*Phragmidium*), clovers (*Uromyces*), blackberries (*Ceoma*), etc. An interesting type is the rust (*Gymnosporangium*) which causes the distortions called cedar apples on the junipers, and the much-branched stunted growths called witches' brooms. This rust has a cluster-cup stage (once named *Rœstelia*) on the hawthorn and apple.

SERIES II. THE TYPICAL BASIDIA FUNGI, OR *EUBASIDIOMYCETES*

276. The Hymenomycetes. This group, which may be considered a sub-class of the Basidiomycetes, comprises all of the higher basidia fungi whose spores are developed on a fruiting surface, called an *hymenium* (meaning a membrane), which is *exposed*. This condition is thus contrasted with that in the Gastromycetes (puffballs, etc.), where the spores are developed within a case. The types of fructification are exceedingly various in this group, which includes the pore, the tooth, and the gill fungi in the various forms of toadstools and brackets. But there are also some simpler types, as the coral fungus (*Clavaria*), with irregular branches (Fig. 234), and also some expanded forms.

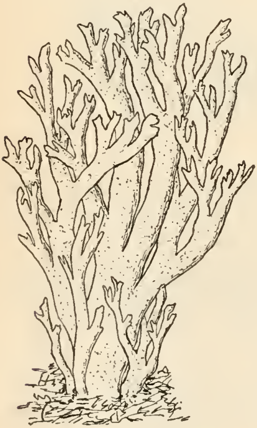

FIG. 234. A coral fungus (*Clavaria*)

The pore fungi. The pore fungi (family *Polyporaceæ*) have commonly the shape of brackets and grow on the trunks of trees, although some are large, fleshy toadstools, as *Boletus* (Fig. 235). The hymenium lines the cavities of the numerous pores which are found on the under surfaces.

Many of the pore fungi are perennial, increasing in size from year to year by adding new layers of growth outside of the old. The bracket or toadstool is merely the fructification which receives its nourishment from an extensive mycelium growing in the wood, and under the bark of trees, or in the soil. Many of the pore fungi are very destructive parasites, greatly injuring and sometimes killing forest trees. They may cause great injury to growing timber.[1] Most of the pore fungi are, however, saprophytic in their manner of life.

FIG. 235. A pore-bearing toadstool (*Boletus*)

The tooth fungi. The tooth fungi (family *Hydnaceæ*) are less common than the pore and gill fungi. Some of them have bracket forms, and some are toadstools (Fig. 236). The fruiting surface is distributed over tooth or spine-like processes.

The gill fungi. The gill fungi (family *Agaricaceæ*) include most of the toadstool and mushroom forms (Fig. 237). A toadstool consists of

FIG. 236. A tooth fungus (*Hydnum*)

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[1] See von Schrenk, "The Decay of Timber and Methods of Preventing It," United States Department of Agriculture, Bureau of Plant Industry, *Bulletin 14*, 1902.

a *stalk* (stipe), which in some genera arises from a *cup* (volva) and is expanded above into the *cap* (pileus). The under surface of the cap bears many thin plates which hang down in a radiating arrangement and are called *gills.* The gills illustrate very well the structure and position of the basidia on a fruiting surface, or hymenium, and cross sections are shown in Fig. 238. It will be seen that the basidia are the swollen terminal cells of a compact mesh of hyphæ, and that each bears a group of four spores on short stalks or sterigmata.

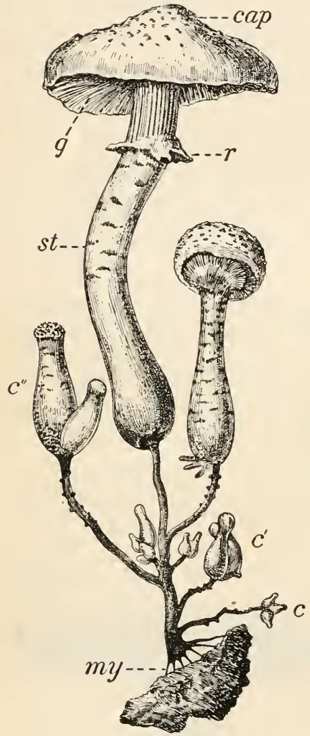

Fig. 237. A group of mushrooms (*Armillaria mellea*)

my, mycelial attachment; *c*, *c′*, *c″*, young stages called buttons; mature mushroom with expanded cap (pileus) shown above; *st*, stem (stipe); *g*, gills; *r*, ring. — After Hartig, through Bennet and Murray

The toadstool is really a fructification. It is attached to an extensive mass of mycelium, which is the vegetative portion of the plant. This mycelium generally lives saprophytically in the soil, frequently around buried roots of trees, but there are some parasitic gill fungi (Plate VI) which cause the decay and final death of valuable timber. The toadstool develops from an accumulation of hyphæ in small structures called *buttons* (Fig. 237, *c*, *c′*, *c″*). The cap region with the gills and stalk become differentiated within the button, and finally break out from the surrounding envelope and expand in a few hours to their full size; hence the expression a "mushroom growth." The remains of the envelope are found in some forms as scales on the top of the cap (see mature mushroom of Fig. 237) and in a ring attached to the stalk below the gills (Fig. 237, *r*), while in certain types (*Amanita*, etc.) there is a large cup (volva) at the base of the plant out of which the stalk rises.

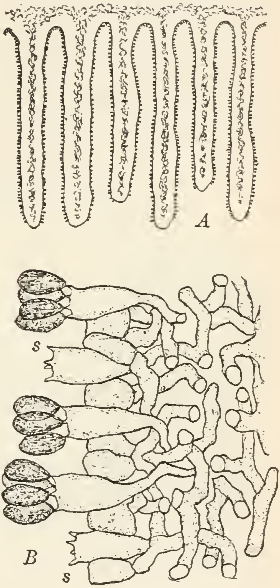

Fig. 238. Gills of mushroom (*Coprinus comatus*)

A, cross section of gills showing fruiting surface (hymenium); *B*, portion of fruiting surface illustrating three basidia with spores and two from which the spores have fallen off, showing the spore-bearing stalks (sterigmata) *s*

It is becoming rather general popular usage to apply the term *mushroom* to all toadstools and other fleshy fungi which are edible. There are no general rules for distinguishing mushrooms from toadstools which do not have exceptions; but the collector may readily learn the characters of the most poisonous species, and likewise become acquainted with a number of choice forms which are easily recognized.[1] It is a good principle, however, to rest satisfied with a knowledge of a few absolutely safe mushrooms and not to experiment with those that are not fully known. The most poisonous species of the gill fungi are in the genus *Amanita* and have large volvas, rings, and white spores, and may be readily recognized when carefully examined. There are also some very poisonous species of *Boletus* among the pore fungi. The commonest mushroom of the market (*Agaricus campestris*) is a form extensively cultivated, but which also grows in the fields. These mushrooms are raised in cellars and caves, in specially prepared, heavily manured beds, which are planted with masses of mycelium called

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[1] See Farlow, "Some Edible and Poisonous Fungi," United States Department of Agriculture, Division of Vegetable Physiology and Pathology, *Bulletin 15*, 1898.

spawn.[1] Some species of *Boletus* are edible, and they, with the morels (Sec. 267) and truffles (Sec. 269), are sold in the European markets with edible gill fungi.

277. The Gastromycetes. This group, in contrast with the *Hymenomycetes*, includes forms in which the basidia line the interior of chambers, or cavities, in the fructifications and are consequently *inclosed* until the fructification matures. Here are found the puffballs, earth stars, nest fungi, and carrion fungi.

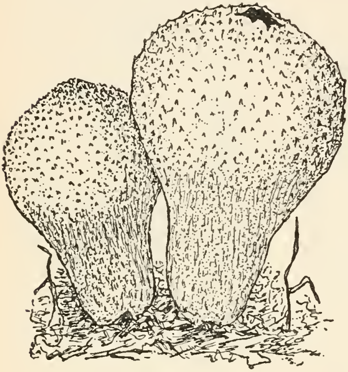

Fig. 239. A puffball (*Lycoperdon*)

The puffballs. These are the fructifications (Fig. 239) of an extensive underground saprophytic mycelium, as in the toadstools and mushrooms. The young puffball has a white flesh made up of hyphæ and filled with small irregular cavities lined with the fruiting surface (hymenium). The spores when ripe lie freely as a brown powder in the dried-up fibrous tissue inclosed in an outer parchment-like envelope. The spores may be discharged through a special opening at the top or scattered by the irregular rupture and decay of the puffball. Young puffballs are edible, and there is one extraordinary species (*Lycoperdon giganteum*) which grows to be a foot or more in diameter and is much prized as a delicacy.

The earth stars. The earth stars (*Geaster*, Fig. 240) are modified forms of puffballs. The envelope is very thick, and the outer portion splits lengthwise into segments which, when wet, curve back from above and raise the fructifications from the ground. In dry weather the segments are usually rolled up

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[1] See Duggar, "The Principles of Mushroom Growing and Mushroom Spawn Making," United States Department of Agriculture, Bureau of Plant Industry, *Bulletin 85*, 1905.

tightly around the fructifications. These movements of the segments in certain species when alternately wet and dry sometimes tear the earth stars loose from the ground so that they may roll about, thus assisting in the distribution of the spores. The puffballs and earth stars are in the same order (*Lycoperdales*).

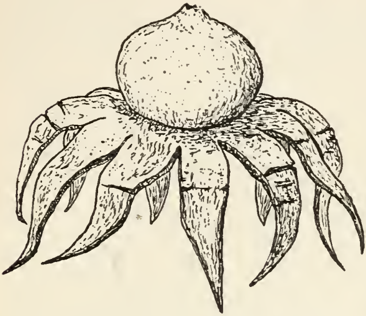

FIG. 240. An earth star (*Geaster*)

The nest fungi. These beautiful little forms (order *Nidulariales*) grow on the earth and decaying wood and when open resemble a nest filled with eggs (Fig. 241). The egg-like structures are portions of the interior of the fructification, and each contains a chamber filled with spores.

The carrion fungi. These very malodorous fungi (order *Phallales*) grow in rich humus and mulchings. They are complicated stalked types first formed within a large globular structure which remains around the base of the stalk as a cup. The top of the stalk bears a dark-colored, sticky mass of spores, that has the odor of carrion and attracts carrion flies, which probably assist in the distribution of the spores.

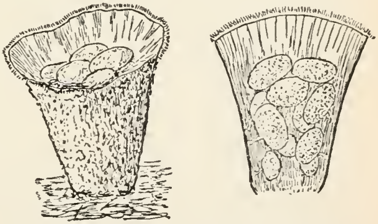

FIG. 241. A nest fungus (*Cyathus*)

The section at the right shows the egg-like structures containing the spores

278. Mycorrhiza. Mycorrhiza (meaning fungus-infected roots) is a remarkable association of the mycelium of certain fungi with the roots of many seed plants, notably trees. The fungal filaments surround the roots with a web (Fig. 242) and enter the outer regions of the root tissue, probably living somewhat parasitically upon the plant as a host. They are in close contact with the soil around the roots, and are believed to be of great assistance to them in their work in the following way. It is necessary for the roots, of course, to establish a close relation to the moisture of the soil in order to obtain water for the green parts of the plant above ground. The surface of the older portions is without root hairs and is surrounded by a hard outer layer which cannot come into very close contact with the minute moist soil particles. But it is thought that the fungal filaments act as root hairs, and perhaps through them the root can absorb a much greater quantity of water and can well afford to give them what nourishment they require in exchange for such valuable services. It is probable that most trees and many others of the larger plants have formed this partnership with the fungi. The kinds of fungi concerned with mycorrhizas are not well understood, but some of them are known to be the mycelia of toadstools and puffballs. The sac fungi also furnish notable examples in the truffles (Sec. 269). The mycorrhiza relationship is an excellent illustration of *symbiosis* (which means a living together), for two organisms exist here in intimate physiological association and both apparently receive benefit from the partnership.

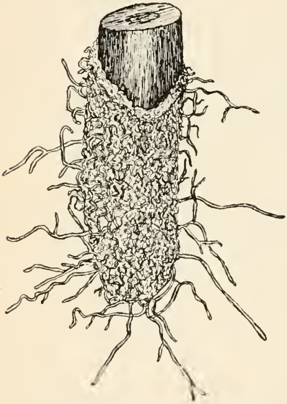

FIG. 242. Mycorrhiza surrounding the tip of a beech root

After Pfeffer

279. Summary of the basidia fungi. The relationships between the different groups of the *Basidiomycetes* cannot be discussed further than to state that the promycelium of smuts and rusts, with its sporidia, is believed to correspond to the basidium with its four spores. There are two small groups called the *jelly fungi* (orders *Auricularales* and *Tremellales*), including the rather common Jew's-ear fungus, whose basidia become divided into four parts. In the Jew's-ear fungus the basidium

Plate VI. A wound parasite (*Pleurotus ulmarius*) on the trunk of a maple tree

After E. M. Freeman

is indeed a four-celled filament resembling the promycelium of a rust, each cell developing a spore at one side on a sterigmata. The winter spores, or teleutospores, of the smuts and rusts are considered to be special resting cells of the fungi, developed to carry these parasitic forms over unfavorable seasons of cold or drought when the host plants are not alive. There is thus a break in the life history at the point where the basidium should normally appear. The germination of these spores continues the life history with the immediate development of a structure (the promycelium) which corresponds to a basidium with its spores.

The higher basidia fungi have apparently lost all trace of sexual organs, but the cluster-cup stage in the rusts is believed to indicate the remains of a modified sexual generation in their life histories. The evidence for this view rests chiefly upon the behavior of the nuclei throughout the life history of the rust and is too complicated for treatment here. The basidia fungi are therefore chiefly, if not wholly, apogamous. The origin and evolution of the *Basidiomycetes* is a problem as yet unsolved, which cannot be here considered. The basidia fungi are, however, by far the most wonderfully varied and specialized assemblage of the fungi.

CHAPTER XXIII

SUMMARY OF THE LIFE HISTORIES AND EVOLUTION OF THE FUNGI

280. The life histories of the fungi. To understand the types of life histories in the different groups of the fungi one must bear in mind the life histories of the most nearly related groups of algæ (Sec. 247), for those of the fungi are based, of course, on the life histories of their algal ancestors. But there have been some very important modifications as the result of the parasitic and saprophytic modes of life of the fungi, and especially because the highest groups of fungi present much sexual degeneration, or apogamy, which of course in some respects simplifies the life histories.

The life history of the bacteria is essentially as simple as that of the blue-green algæ. The alga-like fungi (*Phycomycetes*) is a group, however, whose highest members (the molds, water molds, and blights) have reproductive organs with many points of similarity to the siphon algæ, and more especially to *Vaucheria* (Sec. 228). The sexually formed spores generally develop directly into plants like the parents,[1] so that the formula for the life history is

$$P - < \begin{matrix} g \\ g \end{matrix} > sex.\ s. - P < \begin{matrix} g \\ g \end{matrix} > sex.\ s. - P, \text{ etc.,}$$

the abbreviations g and $sex.\ s.$ standing for gamete and sexually formed spore, respectively. There is often extensive reproduction through various forms of asexual spores between successive sexual generations. And indeed sexual organs may only be formed at rare intervals, as in the bread mold, or they may

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[1] They form zoöspores, however, in some of the blights.

not be functional so that a condition of apogamy is present, as in the water molds.

The life histories of the sac fungi (*Ascomycetes*) are especially interesting in relation to those of the red algæ (Sec. 246). It is known in regard to a number of types that the sac fruits (ascocarps) develop as the result of a sexual process, corresponding in this respect to the cystocarps. The ascospores are formed at the end of the ascocarp phase of the life history just as the carpospores are formed at the end of the cystocarp phase in the red algæ. Both ascocarps and cystocarps are, then, new generations developed between and alternating with the sexual plants. They are sporophytes alternating with gametophytes. The formula for the life history of a sac fungus with functional sexual organs is then

$$G<_{g}^{g}> - S\ \text{(ascocarp)} - \textit{asex. s.}\ \text{(ascospore)}$$

$$- G<_{g}^{g}> - S - \textit{asex. s.} - G,\ \text{etc.,}$$

G and S standing for gametophyte and sporophyte, respectively, and *asex. s.* for asexual spore.

It must always be remembered, however, that the sac fungi have a great variety of methods of asexual reproduction through conidia, etc. Consequently sexual organs may be formed only occasionally, as in the green mildew (*Penicillium*). There is also probably much apogamy in the group, so that the sac fruits are apogamously developed.

The basidia fungi present the remains of an alternation of generations in the rusts somewhat similar to that of the sac fungi. The cluster cups are believed to be the beginning of a phase that formerly followed a sexual process just as do the ascocarps and cystocarps. However, the male organs (spermogonia) of the rusts are no longer functional, and the cluster cups must be considered as developing apogamousy, although there is now a complicated history substituted for the original sexual process. The cluster-cup stage is omitted entirely in some of the rusts and in all of the smuts, and there are likewise no traces of it in the higher basidia fungi (*Eubasidiomycetes*). Sexual degeneration in these forms, then, has apparently been carried so far that the sexual organs have disappeared entirely from the life histories.

281. The origin and evolution of the fungi. The study of the evolution of the fungi must be taken up for each of the larger classes separately, for there is every probability that each has had an independent origin from widely separated groups of the algæ. The bacteria have probably been derived from the blue-green algæ. The higher alga-like fungi (molds, water molds, and blights) apparently show relationships to the siphon algæ. Some authors believe that the sac fungi have come from the red algæ. The origin of the basidia fungi is very much in doubt and that of the yeasts also, although it is generally held that the latter are degenerate forms from some of the higher fungi. The evolution of the fungal forms in each group becomes very complicated, because the fungi have such wonderfully varied habits resulting from their parasitic and saprophytic ways of living. In fact, these life habits have produced the greatest variety of structures and adaptations known in any group of spore plants. Still more remarkable, perhaps, is the widespread tendency towards sexual degeneration, which is also believed to be associated with the parasitic and saprophytic life habits.

CHAPTER XXIV

THE BRYOPHYTES AND THE ESTABLISHMENT OF ALTERNATION OF GENERATIONS

282. The bryophytes.* The division *Bryophyta* (meaning moss plants) is the next great group of plants above the division *Thallophyta* (Chapter XIX), and includes two classes: (1) the liverworts, or *Hepaticæ*, and (2) the mosses, or *Musci*. It is not best to define these classes until the structure and life histories of types from each group have been studied. Furthermore, it is impossible fully to understand the characters of the bryophytes and thallophytes except when compared with one another. Accordingly these matters have been reserved for the final section of this chapter under the heading Summary of the Bryophytes and Thallophytes (Secs. 300, 301).

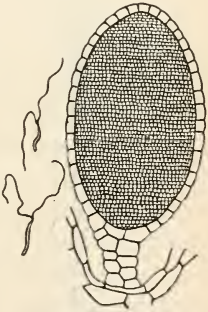

FIG. 243. The antheridium of a liverwort (*Marchantia*)

Antheridium in section, showing the outer capsule and the mass of small cells within, in which are developed the minute two-ciliate sperms shown at the left. — After Sachs

However, the bryophytes differ from the thallophytes in two very important respects which may be briefly stated at once, for they must be thoroughly comprehended in order to understand the life histories of the liverworts and mosses. They can only be made clear when illustrated through laboratory studies. These two differences are (1) in the *sexual organs*, which are many-celled, and (2) in the appearance of a new stage in the life cycle called the *sporophyte*.

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* TO THE INSTRUCTOR: The introduction to this chapter assumes that the life history of a liverwort or moss has been studied in the laboratory.

283. The sexual organs. The sexual organs of the bryophytes are *many-celled.* They are male and female and each consists of a cellular case, or capsule, in which are formed the respective gametes, which are sperms and eggs. It will be remembered that the sexual organs of the thallophytes are, with very few exceptions, one-celled. The conspicuous exceptions are the plurilocular sexual organs of the lower brown algæ (see *Ectocarpus*, Sec. 235) and the antheridium of the stoneworts (Sec. 230).

The sperm-producing organ, or antheridium. The *antheridium* (Fig. 243) is a stalked, oval or elliptical structure, with an outer cellular envelope inclosing a dense mass of very small cubical cells in which are developed the sperms. The sperms are minute elongated or slightly coiled protoplasts, with a pair of cilia at one end. The mature antheridia only discharge their sperms when wet, as after heavy rains or dews, and the sperms then swim about in the moisture. At these times the plants are practically leading an aquatic life like their algal ancestors, and the development of motile sperms in these land plants shows clearly that they must have come from forms with aquatic life habits.

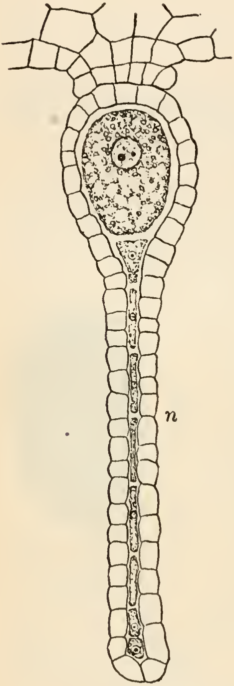

FIG. 244. The archegonium of a liverwort (*Marchantia*)

The archegonia in this genus hang down from a special receptacle (Fig. 251). The large egg is shown in the swollen base of the archegonium, while the neck *n* contains a row of canal cells which break down into mucilage as the archegonium matures.

The egg-producing organ, or archegonium. The female organ is called an *archegonium.* It is flask-shaped (Fig. 244), and the outer cellular envelope incloses at maturity a row of cells. The cell situated in the enlarged portion of the archegonium (venter) becomes the single egg, while the others in the neck region (Fig. 244, *n*), called *canal cells*, break down and their substance becomes changed into mucilage. The archegonia, like the antheridia, open only when wet, the cells at the tip separating so as to give a clear passage for the entrance of the sperms into the neck. The sperms are attracted to the opening by certain substances such as sugar contained in the liquefying mucilage. The sperms swim down the neck, and one of them, fusing with the egg, fertilizes it. There is much evidence that the canal cells are degenerate gametes, and that the archegonium came from a type of sexual organ that originally produced a number of gametes, as does the antheridium.

284. The sporophyte. The term *sporophyte* has appeared before in the accounts of the red algæ (Sec. 246) and sac fungi (Secs. 266, 272) where certain peculiar fructifications (cystocarps and ascocarps), following the sexual process, alternated with the sexual plants. The sporophytes of the liverworts and mosses have a similar position in the life history, and are likewise borne on the parent plants and frequently called their “fruits.”

The sporophyte of the liverworts and mosses develops at once from the fertilized egg, which never becomes a resting spore (oöspore), as in the algæ. The form is various in different groups. Most of the mosses have long, stalked sporophytes (Figs. 261, 265), which end in swollen spore cases. The liverworts generally have much smaller sporophytes, some of which have no stalk at all and consist of the spore case alone. If the sporophyte is small it may remain inclosed in the base of the archegonium, which becomes much enlarged. But the stalked sporophytes either burst out of the archegonium, or frequently, as in the common mosses, tear it off and carry it upwards as a cap-like structure (Fig. 265, *B*, *cal*) called the *calyptra* (meaning a veil). The sporophytes always remain attached to the parent plant, and finally develop spores asexually in the spore cases. The spores are formed in groups of four, called *tetrads*, within spore mother cells (Figs. 245, *B*, *s*; 258, *B*). These asexual spores have heavy walls and can survive the winter, frequently protected by the spore case. It will be remembered that in the algæ the sexually formed spore is generally the protected resting spore.

285. Alternation of generations. There are thus two phases in the life history of a liverwort or moss. First, there is the plant which bears the sexual organs, and this is called the *gametophyte* (meaning a gamete-bearing plant); second, there is the structure which arises from the fertilized egg and ends its history by developing asexual spores, and for this reason it is called a *sporophyte* (meaning a spore-bearing plant). The gametophyte is developed from the spore, and the sporophyte from the fertilized egg. So there is a regular alternation of these two phases in the life history, the gametophyte producing sexual cells, or gametes, and the sporophyte producing asexual spores. The two phases are regarded as separate generations because each has its origin from a distinct kind of reproductive cell (egg or spore). The gametophyte is of course a sexual generation and the sporophyte an asexual one. Their following one after the other makes an *alternation of generations*,—a phrase which from now on will be frequently used, because it signifies the most remarkable feature in the evolution of all plants above the thallophytes. The simple sporophytes of ancient bryophytes gave rise to the fern plants and through them to the large and complicated seed plants.

A life history which consists of an alternation of sporophyte and gametophyte, as in the liverworts and mosses, may be expressed by the formula

$$\textit{Gametophyte} < \substack{\textit{sperm} \\ \textit{egg}} > - \textit{Sporophyte} - \textit{asexual spore} - \textit{Gametophyte}, \text{ etc.}$$

This in an abbreviated form becomes

$$G < \substack{s \\ e} > - S - sp - G < \substack{s \\ e} > - S - sp - G, \text{ etc.}$$

One must bear in mind these general characters of the bryophytes, as the liverworts and mosses are separately taken up and their characters finally summarized by treating the subjects under the four heads:

Class I. The liverworts, or *Hepaticæ*
Class II. The mosses, or *Musci*.
The origin and evolution of the bryophytes.
Summary of the bryophytes and thallophytes.

CLASS I. THE LIVERWORTS, OR *HEPATICÆ*

286. The liverworts. The liverworts grow most luxuriantly in moist and shaded situations, some forms on the ground, some on rocks, and some on trees. There are also certain aquatic liverworts which float on the surface of the water, and a few very simple ones which are entirely submerged like the algæ. Thus, although most of the types have the land habit, some show very clearly adaptations for the aquatic life of their ancestors among the algæ. The creeping habits of the liverworts probably indicate the way in which land plants arose and became established first along the margins of streams, ponds, and marshes where algal growths emerged from the water or were left stranded on the wet earth. These first land liverworts naturally clung close to the wet earth in the beginning, until the development of root-like systems of filaments (rhizoids), which could gather moisture, permitted them to develop upright stems as in the mosses. The forms of the liverworts are various, as will appear in the following brief account of the four orders.

287. The Riccia group. The simplest liverworts (order *Ricciales*) have a flat plant body (gametophyte), some forms floating on the surface of the water and others submerged, while certain types grow close to moist earth. The plant body is a true thallus (Fig. 245, *A*), and indeed is much simpler than the plant bodies of many thallophytes among the brown and red algæ. The lower surface of the thallus bears numerous filaments, called *rhizoids* (from their resemblance to roots), and delicate membrane-like fringes, which draw up water from the soil like root hairs if the plant has the land habit. The thallus grows from a number of points (Fig. 245, *A*, *gp*) situated in notches at the ends of lobes which fork in pairs and finally split apart, so that the plants multiply very rapidly during the vegetative season. The sexual organs are borne on the upper surface of this gametophyte, and the sporophyte is a simple globular case (Fig. 245, *B*), filled with spores, which remains inclosed in the base of the archegonium, so that the spores are not set free until the decay of the plant.*

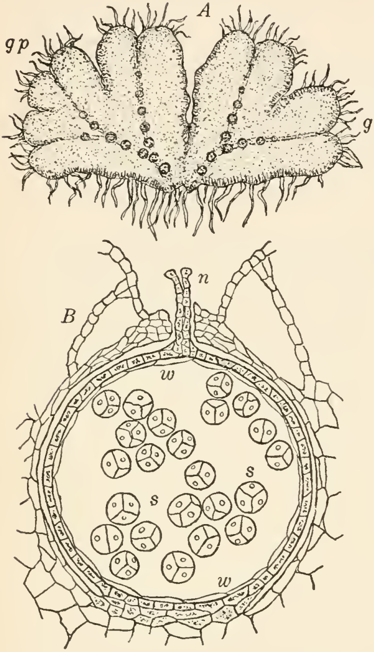

Fig. 245. A floating liverwort (*Ricciocarpus*) and its sporophyte

A, habit sketch of the sexual plant (gametophyte) viewed from above, showing the position of the sporophytes in lines back of the growing points *gp*. *B*, section of a sporophyte contained within the parent archegonium, whose neck *n* is still present: *s*, spores in groups of four (tetrads) within the spore mother cells; *w*, remains of the wall of the sporophyte

288. The Marchantia group. This large group (order *Marchantiales*) is well represented by the common liverwort (*Marchantia polymorpha*), which grows on the ground in moist situations. The ribbon-like thallus of species of *Marchantia* (Fig. 246) forks regularly, but one of the branches is

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* To the Instructor: These points are admirably illustrated in the large floating form (*Ricciocarpus natans*), which is not uncommon and is an excellent type for laboratory study, although *Marchantia* is the form most generally used.

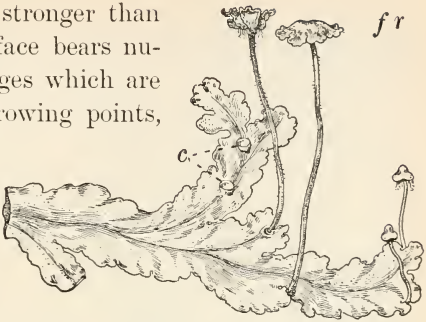

Fig. 246. A *Marchantia* form (*Marchantia disjuncta*)

fr, female receptacle; *c*, cups producing buds. — After Sullivant

almost always larger and stronger than the other. The lower surface bears numerous filaments and fringes which are formed in front of the growing points, protecting them, and later become distributed along the lower surface. The upper surface is marked by diamond-shaped areas (Fig. 247, *A*) which show the position of curious large air chambers (Fig. 247, *B*) that contain very numerous filaments whose cells have well-developed chloroplasts. These filaments perform

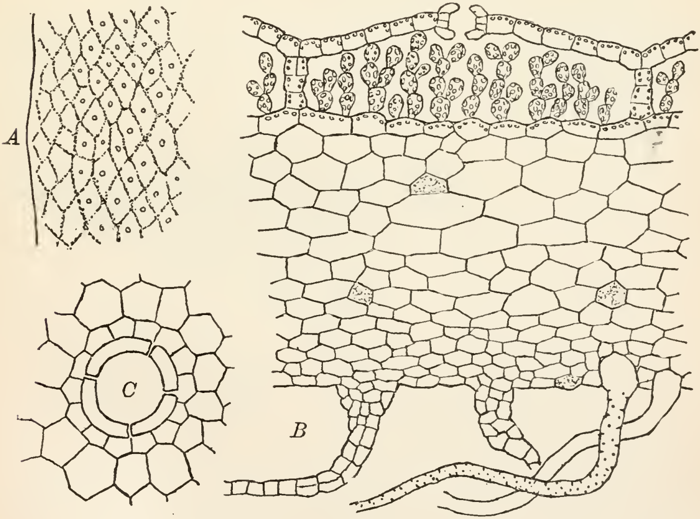

Fig. 247. Structure of the thallus of *Marchantia*

A, surface of thallus, the diamond-shaped areas marking air chambers; *B*, a section through the middle region of the thallus showing air chambers above, filled with branching green filaments, and the fringes and root-like hairs (rhizoids) on the lower surface; *C*, surface view of the pore which opens into an air chamber the greater part of the chlorophyll work (photosynthesis) of the plant, and the chambers are developed as protective structures around them. Each chamber is open above to the air by a circular pore (Fig. 247, *C*), which can be easily seen in the center of each diamond-shaped area. This specialization of the upper surface of the *Marchantia* plant to a light relation gives it a general resemblance to the cell structure of leaves in seed plants and ferns.

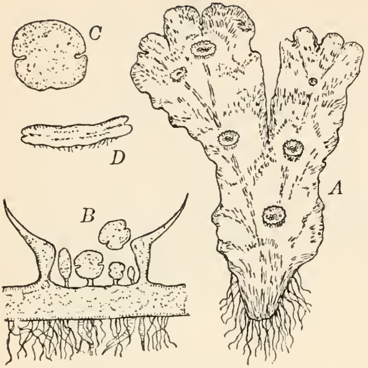

FIG. 248. The cups and buds of *Marchantia*

A, cup-bearing plant; *B*, section of a cup showing the buds arising from its bottom; *C*, a bud showing the two growing points; *D*, young plant developing from the bud

Some individuals of *Marchantia* (Fig. 248, *A*) will usually be found bearing *cups* (cupules) which contain numerous green bodies. These are many-celled reproductive organs, called *buds* (gemmæ), which develop from the bottom of the cup (Fig. 248, *B*). Each bud has two notches at opposite sides (Fig. 248, *C*), which become two growing points when the structure falls on its side upon damp earth and begins to grow (Fig. 248, *D*). This is a characteristic and very successful method of rapid asexual multiplication in *Marchantia*.

The sexual organs of *Marchantia* are developed

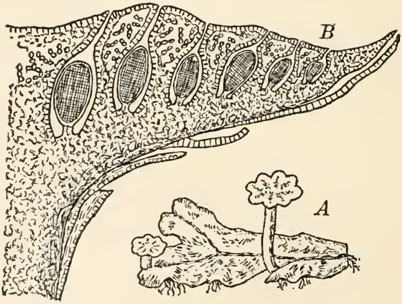

FIG. 249. The male plant of *Marchantia*

A, male plant bearing antheridial receptacles; *B*, lengthwise section of a receptacle (semidiagrammatic), showing a row of sunken antheridia upon the upper surface; the youngest lie just back of the notches in the receptacle, which are the growing points; air chambers are also shown on the upper surface

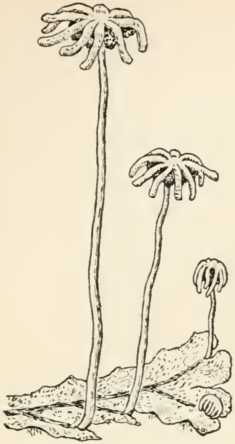

Fig. 250. Female plant of *Marchantia*

Showing the umbrella-like archegonial receptacles in various stages of development

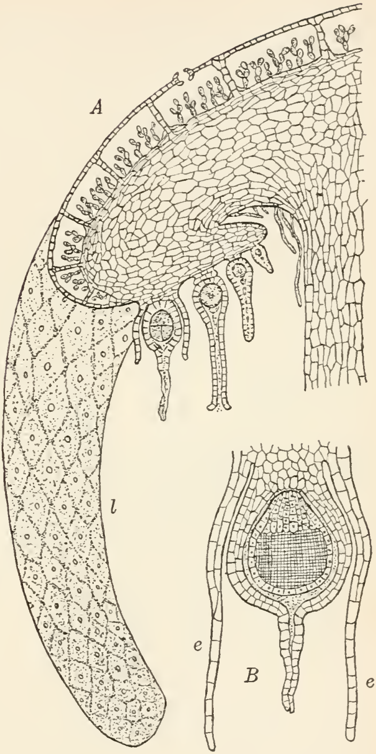

Fig. 251. The female receptacle of *Marchantia*

A, portion of a lengthwise section of a young receptacle (semi-diagrammatic), showing a row of archegonia hanging down from the lower surface, the youngest being nearest the stalk: air chambers are present on the upper surface; *l*, one of the finger-like lobes back of the section, the diamond-shaped areas indicating air chambers. *B*, a young sporophyte within the parent archegonium: the region which is to become the spore case is indicated by the cross lines, and the small foot is attached to the base of the archegonium; *e*, a special envelope developed around the archegonia of *Marchantia*

on stalked, umbrella-like receptacles, which are really much-modified branches of the thallus. They bear either antheridia or archegonia, and the two sexual organs are not found together on the same plant. The antheridial receptacle (Fig. 249, *A*) is shorter than the archegonial, and the top is a flattened disk with a lobed or scalloped margin. The antheridia (Figs. 243, 249, *B*) lie in cavities or pits along radiating lines on the upper surface of the receptacle, and the youngest antheridia are found nearest the notches which mark the position of the growing points along the edge of the disk. The archegonial receptacle (Fig. 250) is larger than the antheridial, and the top is bent back into several long, finger-like projections like the ribs of an umbrella. Numerous archegonia are formed in lines (Fig. 251, *A*) on the under side between the lobes, and are protected by singular fringes. The youngest archegonia are formed nearest the stalk, so that the older ones lie farther out, — an arrangement exactly opposite from that of the antheridia. This is explained by the fact that the growing points which lie between the lobes grow downward and underneath towards the stalk. The edge of the disk is thus bent back on itself, and the lower surface is really an extension of the upper surface.

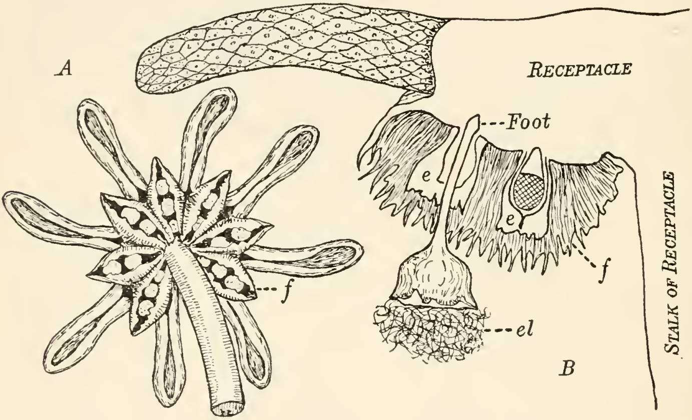

FIG. 252. Sporophytes and receptacles of *Marchantia*

A, lower view of an old female receptacle, showing the sporophytes in rows between the fringes *f*, like peas in a pod. *B*, section of a receptacle (diagrammatic), showing a mature sporophyte anchored by its foot and projecting beyond the fringe *f*: the spore case is open, exposing the mass of elaters *el*; a young sporophyte is shown at the right still inclosed within the archegonium (calyptra); *e*, special envelopes around the archegonia and sporophytes

A number of archegonia may be fertilized in *Marchantia*, and their eggs then develop sporophytes in radiating rows on the lower surface of the receptacle (Fig. 252, *A*) between the fringes. The sporophyte is more complex than in the *Riccia* types. The lower part (Figs. 252, *B*; 253, *A*) becomes a small organ of attachment to the gametophyte, called the *foot*, through which it obtains water with food in solution. The upper part becomes a *spore case*, developing numerous spores, and among them spirally marked filaments, termed *elaters* (Fig. 253, *B*), which are stiff and elastic and help to distribute the spores. The elaters are developed from cells in the young spore case. The spore case is carried beyond the fringe of the receptacle (Fig. 252, *B*) by the elongation of the region above the foot, which forms a *stalk*. The presence of a foot and stalk in addition to the spore case marks a decided advance over the simple sporophytes of the *Riccia* types, which consist of the spore case alone.

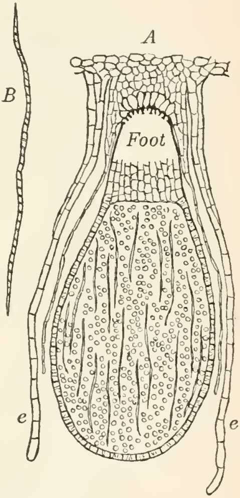

Fig. 253. The sporophyte of *Marchantia*

A, longitudinal section of sporophyte showing spore case and foot attached to the base of the archegonium: *e*, a special envelope. *B*, an elater

It is very important to note that the sporophyte has this close attachment to the gametophyte and is dependent upon it for water and food in solution, because it shows that the sporophyte of the liverworts really lives in large part like a parasite upon the gametophyte as a host.

289. The Jungermannia group. This assemblage (order *Jungermanniales*) is very much the largest group of the liverworts and contains more than three thousand species. They are known as the leafy liverworts because most of them have long stems, with delicate, moss-like leaves. The leafy liverworts are frequently mistaken for mosses, since they are common on tree trunks and in shaded situations. But they have a creeping habit, and there are two crowded rows of large leaves (Fig. 254, *A*), one on each side of

Fig. 254. The female plant of a leafy liverwort (*Porella*)

A, habit sketch of the upper surface, with the two rows of leaves at the sides; *B*, a portion of lower surface, showing the third row of small leaves (amphigastria); *C*, the stalked sporophytes with open spore cases *sc*; *D*, a sporophyte with the spore case split lengthwise into four parts. — After Campbell

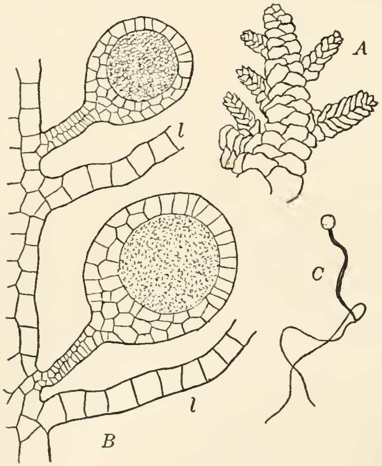

Fig. 255. The antheridia of a leafy liverwort (*Porella*)

A, portion of male plant, illustrating the small antheridial branches at the side; *B*, section of an antheridial branch, showing two antheridia situated just above the attachment of the leaves *l*; *C*, the much-elongated sperm, with the two cilia at one end and the remains of the parent cell at the other. — *C*, after Campbell the stem, and a third row of small modified leaves on the lower surface (Fig. 254, *B*). The stems of mosses, on the contrary, are almost always upright, and the leaves are arranged radially, so that the stem has no upper or lower surface.

The antheridia of the leafy liverworts are borne singly along the stem at the bases of the lateral leaves (Fig. 255, *B*) on certain branches which are frequently much smaller than the vegetative shoots (Fig. 255, *A*). The archegonia are developed in clusters at the ends of branches.

The sporophyte (Fig. 256, *A*) has a stalk which elongates rapidly just before the spores are ready to be shed, so that the spore case is raised above the gametophyte (Fig. 254, *C*), as in the mosses. However, the spore case is much less complex than that of the mosses, being a simple capsule that splits lengthwise into four parts at maturity (Fig. 254, *D*). There are spirally thickened filaments, or elaters (Fig. 256, *C*), among the spores, as in *Marchantia*, and these structures are not found in the mosses. The foot of the sporophyte (Fig. 256, *A*) is always well developed in the leafy liverworts.*

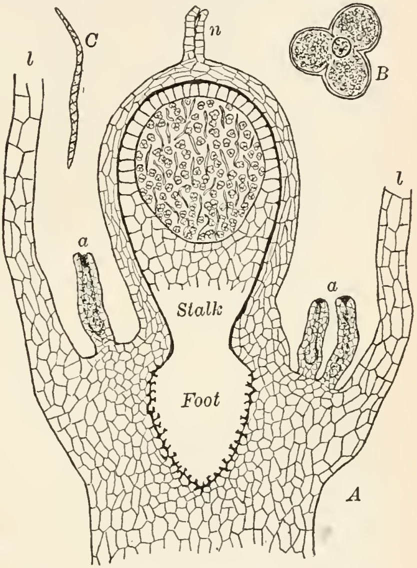

FIG. 256. The sporophyte of a leafy liverwort (*Porella*)

A, section of a sporophyte still contained within the parent archegonium, whose neck *n* is shown above, the foot deeply sunken in the tissue of the gametophyte: *a*, archegonia of the terminal group, which were not fertilized; *l*, leaf-like envelopes. *B*, the four-lobed spore mother cell, which develops four spores (tetrad). *C*, an elater

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* TO THE INSTRUCTOR: Good material of the leafy liverworts frequently furnishes better subjects for type study of the liverworts than *Marchantia*.

290. The Anthoceros group. These types (order *Anthocerotales*) are considered the highest of the liverworts because of their more complicated sporophytes. The gametophytes are thalloid (Fig. 257), somewhat irregular in outline, and more simple in structure than those of *Marchantia.* The sporophytes are an inch or more in height, and grow up from the gametophyte like blades of grass. The upper portion splits lengthwise into halves at maturity.

The spores of *Anthoceros* do not all mature at once, as in other liverworts, but new spores are formed at the base of the sporophyte as the older mature (Fig. 258, *A*), and there is a continuous elongation of the structure during the summer from a basal region of growth. The cells composing the wall of this long sporophyte contain large single chromatophores (Fig. 258, *E*), and there are breathing pores, or stomata (singular, *stoma*, meaning a mouth), on the surface (Fig. 258, *D*), which lead into intercellular spaces in the green tissue beneath. Consequently the sporophyte is able to manufacture its own food by photosynthesis, as any green plant may do. But it depends upon the gametophyte for its supply of water, which is absorbed through a large bulbous foot (Fig. 258, *A*) that is deeply imbedded in the thallus of the gametophyte.

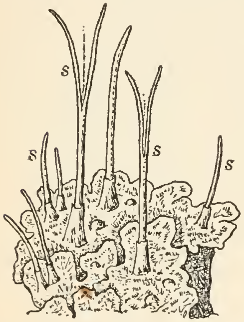


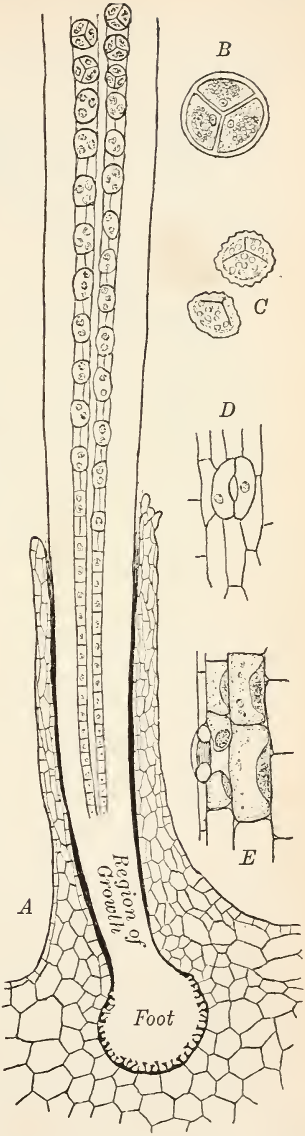
Fig. 257. Habit sketch of *Anthoceros*

The thalloid sexual plants (gametophytes), with the sporophytes *s* in various stages of development

If the base of this sporophyte could establish a root-like structure growing in the soil, it might live independently of the parent gametophyte, for it has chlorophyll-bearing tissues in communication with the air through stomata, just as in the ferns and seed plants. And it has also the power of indefinite growth from its basal region (Fig. 258, *A*), limited only by the length of the summer season. These peculiarities of the sporophyte of *Anthoceros* are very suggestive of the way in which higher plants must have arisen from forms somewhat like the liverworts, a subject which we shall consider later in our account of the ferns (Sec. 331). Of all the bryophytes, this seems to be the genus which most closely approaches the higher plants. This account of plant evolution is now well started towards the higher conditions of plant development, namely, those of the ferns and seed plants whose sporophyte generations are independent plants with roots, stems, and leaves, and which comprise the most independent and successful vegetation on the earth.

CLASS II. THE MOSSES, OR *MUSCI*

291. The mosses. The mosses are very much more numerous than the liverworts. Some of the common kinds grow in extensive carpets on hillsides and in forests, becoming important factors in the plant



A, longitudinal section (semi-diagrammatic) through the base of the sporophyte, showing the large foot imbedded in the tissue of the gametophyte, the region of growth, and the spore-producing tissue which forms a cylinder in the center of the stalk; *B*, a group (tetrad) of four spores (three shown) in a spore mother cell; *C*, spores; *D*, a stoma viewed from the surface; *E*, section through a stoma, showing cells with large single chromatophores under the surface layer (epidermis)

FIG. 258. The sporophyte of *Anthoceros*

formations of many regions. The peat mosses are the chief inhabitants of certain kinds of bogs and pond margins. The mosses therefore constitute a group of considerable importance in the plant population of the earth, while the liverworts are for the most part confined to rather special life habits and, with the exception of the leafy liverworts, are not rich in species or numerous in individuals. Almost all of the mosses fall into two groups, which may be called the *peat mosses* and the *common mosses.*

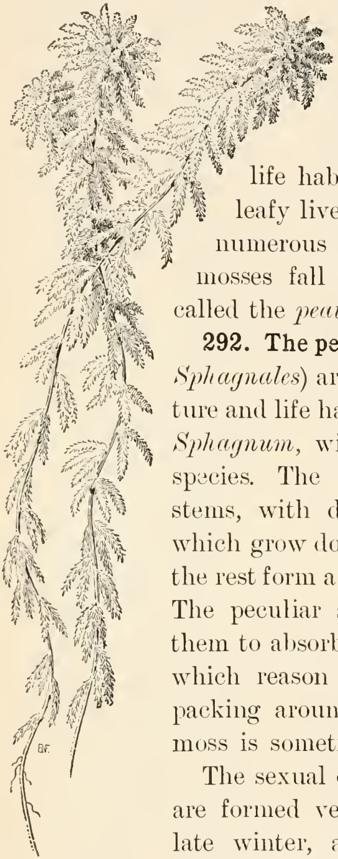


Fig. 259
The peat moss
(*Sphagnum*)

292. The peat mosses. The peat mosses (order *Sphagnales*) are very remarkable for their structure and life habits. There is only a single genus, *Sphagnum*, with about two hundred and fifty species. The plants (gametophytes) have long stems, with delicate, leafy branches, some of which grow downward and soak up water, while the rest form a dense cluster at the top (Fig. 259). The peculiar structure of these mosses allows them to absorb and hold water like a sponge, for which reason they are used by gardeners for packing around plants and flowers. The dried moss is sometimes used for bedding in stables.

The sexual organs (antheridia and archegonia) are formed very early in the spring or in the late winter, and the fertilization of the egg leads at once to the development of a sporophyte. The sporophytes are large, smooth capsules (Fig. 260, *A*), which appear to have stalks, but these are really special developments of the gametophytes. The spore case is attached to the top of the stalk by a large foot and opens by a cover (Fig. 260, *B*, *c*), which falls off. The spores on germination produce small flat cell plates, out of which the leafy peat mosses arise from special buds. These cell plates suggest the simple thalloid gametophytes of the liverworts, and the leafy structure is perhaps a special development from them.

The peat mosses live in bogs and swamps and are especially common in northerly regions and in the mountains, where they grow over wet rocks, sometimes covering large areas. They develop so rapidly that they frequently fill ponds and bogs. The first growth is around the edges of the pond, but this gradually works inward, until finally the whole surface is covered with peat moss. Such conditions produce quaking bogs, for the surface is not firm enough to hold any large animal which might walk upon it. Quaking bogs become firmer as the lower

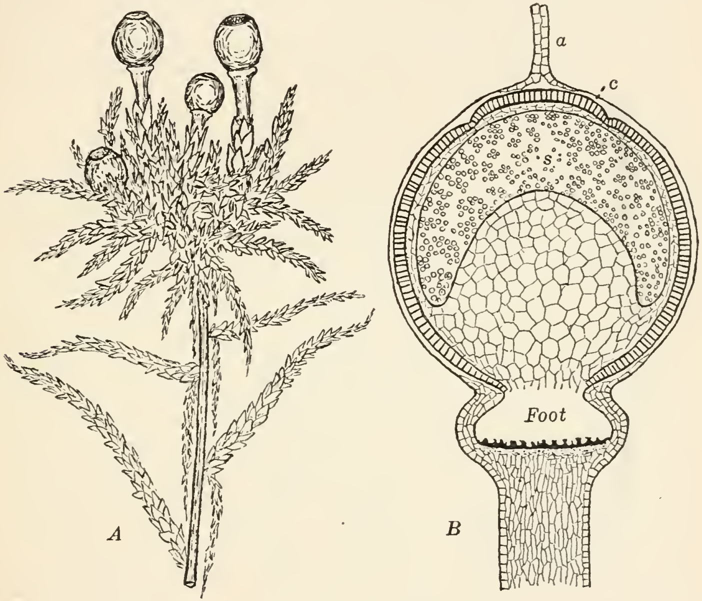


FIG. 260. The sporophyte of the peat moss (*Sphagnum*)

A, group of the sporophytes on stalks, which are really growths from the gametophyte. *B*, longitudinal section through a sporophyte, showing the large foot imbedded in the top of the stalk: *a*, the remains of the parent archegonium, with the neck still present; *s*, spore chamber; *c*, cover parts of the peat mosses die and form a fibrous deposit below. These deposits may grow to be many feet in thickness, and finally become so firm that they can be cut out in blocks. Such blocks when dried are used for fuel, especially in Ireland and in the Highlands of Scotland. There are regions of the northern United States, Canada, Europe, and Asia where the peat mosses cover immense territories, and there are innumerable bogs filled with deposits of peat which may sometime become important sources of fuel supply.

Peat bogs are generally poorly drained or not drained at all, and the water becomes very rich in certain organic acids that result from the partial decomposition of the vegetation. The accumulation of these acids renders the water unfit for the growth of bacteria and is largely responsible for the preservation from decay not only of the remains of the peat mosses but of other plants with them. It is said that whalers and other ships from the New England coast when starting on long voyages preferred to take their supplies of drinking water from peat bogs because of its keeping qualities. Occasionally the bones of extinct animals, such as the mammoth and mastodon, are found in peat, since these gigantic creatures became mired in the soft bogs of former periods.

As a quaking bog becomes firmer, other plants begin to grow among the peat mosses. Certain grasses appear, some characteristic orchids (*Calopogon*, *Pogonia*, *Arethusa*, *Cypripedium*, etc.), the insectivorous plants *Sarracenia* (Fig. 311) and *Drosera* (Fig. 312), such heaths as the swamp cranberry, swamp blueberry, swamp azalea, and Labrador tea, and certain trees, as the larch or tamarack (*Larix*), black spruce (*Picea*), the arbor vitæ (*Thuya*), and the white cedar (*Chamæcyparis*). These plants, in various combinations with the peat mosses, form very characteristic associations, and they furnish some of the best illustrations of what the ecologist calls *plant formations*. The northeastern United States and Canada are full of examples of this interesting feature in the natural history of the *Sphagnum* swamp.

293. Common mosses.* The common mosses (order *Bryales*) are familiar because of the occurrence of numerous species with conspicuous upright stems, which develop the long-stalked sporophytes with characteristic terminal spore cases (Figs. 261, 265). It is a very large group, containing over eight thousand species, and is by far the most numerous assemblage in the bryophytes. These mosses grow in the greatest variety of situations, — in swamps and bogs, in the water of streams, in moist and shaded woods, in open fields, and on relatively dry hillsides and rocks. They perform an important service to plant life in holding back much of the rainfall, allowing it to sink into the earth

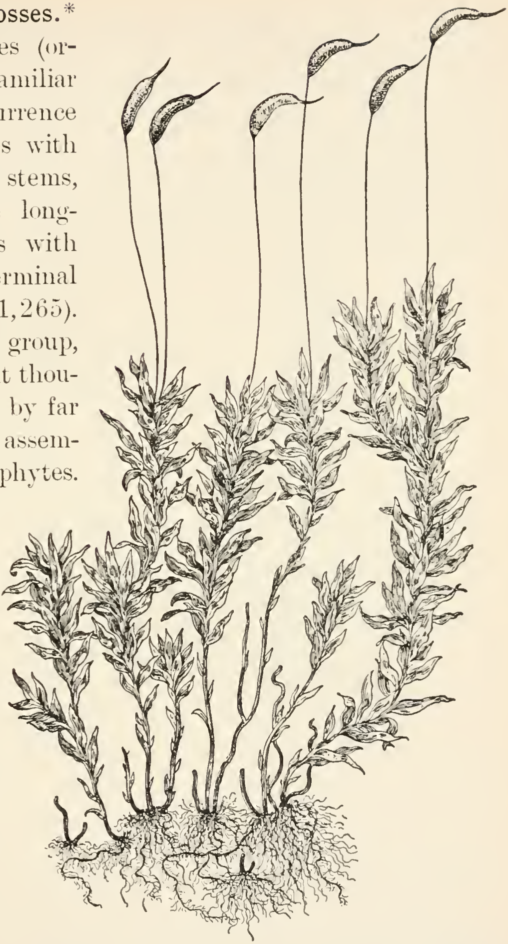


Fig. 261. A common moss (*Catharinea undulata*)

Showing the branching leafy moss plants (gametophytes) attached to the root-like mass of protonemal filaments and bearing sporophytes. — After Sachs

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* To the Instructor: In a short course it is best to present the life history of bryophytes through a somewhat detailed study of one of the common mosses, followed by general studies of a variety of forms of mosses and liverworts.

instead of running rapidly off in floods. The lichens and mosses are among the first plants to appear on barren soil or exposed rocks and cliffs, and are also the plant pioneers that push their way up mountains and into the arctic regions where no other vegetation can live.

294. The life history of a moss. The life history of the common mosses is more complex than that of a liverwort. The moss spore does not develop directly into the leafy moss plant. It produces a preliminary filamentous growth, called the *protonema* (meaning preliminary thread), which sometimes forms an extensive network over the ground, resembling at first sight such terrestrial algæ as certain species of *Vaucheria*. The protonemal filaments (Fig. 262), however, consist of cells placed end to end (they are never cœnocytic); they have generally oblique cross walls and contain numerous disk-shaped chloroplasts. There are no algæ known which the protonema resembles in detail, and yet this phase in the life history suggests what may have been the life habits of ancestors of the mosses. Certain cells of

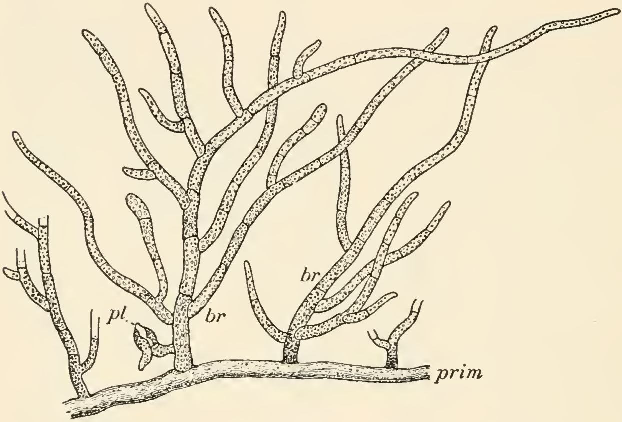

FIG. 262. The protonema of a common moss (*Funaria*)

prim, primary shoot; *br*, branches from primary shoot; *pl*, young moss plant or bud. — After Sachs the protonema change their methods of cell division and develop small buds (Fig. 262, *pl*) which grow into the leafy moss plants (Fig. 263). One moss spore may give rise to a great quantity of protonema, which by means of the numerous buds will form a large group or even a turf of moss plants. Therefore the protonema is a very effective means of establishing the large carpets of moss vegetation. The leafy moss plant develops the sexual organs in clusters at the top of the stem and has further peculiarities of structure which will be described later. The protonema together with the leafy moss plant constitute the sexual or gametophyte phase of the life history.

The fertilization of an egg in an archegonium starts at once the development of the sporophyte, often called the moss fruit. The fertilized egg gives rise to a many-celled structure (Fig. 264, *A*), which establishes a growing point above and a foot attachment to the gametophyte below. This young sporophyte is contained at first entirely within the parent archegonium, which enlarges with its development (Fig. 264, *B*, *a*). But finally the growth of the sporophyte is so rapid that the archegonium is torn away at its base and borne upwards on the elongating stalk of the sporophyte. The remnant of the archegonium then covers the tip of the stalk like a cap (Fig. 265, *B*, *cal*) and is called the *calyptra* (meaning a veil), which must serve a useful purpose, protecting the delicate growing tip of the sporophyte. Finally, the tip of the sporophyte enlarges and becomes the complex spore case

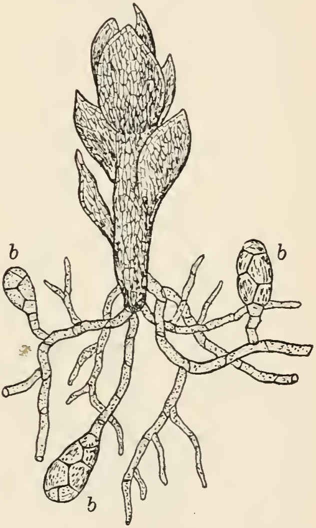

FIG. 263. A young plant of a common moss (*Webera*)

Showing its attachment to the protonemal filaments which bear reproductive buds *b*

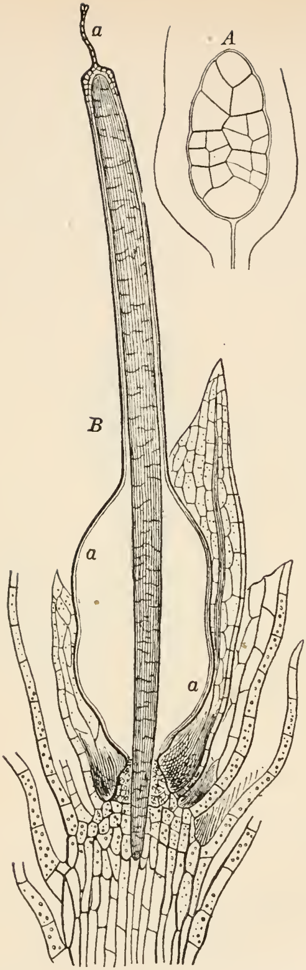

Fig. 264. Developing sporophytes of a common moss (*Funaria*)

A, very young stage, showing the early cell divisions of the egg; *B*, older sporophyte just before the archegonium *a* is torn away from the gametophyte and carried upward as the calyptra. The base of the sporophyte has now grown down into the tip of the leafy moss plant (gametophyte) and is firmly anchored to it. — After Sachs

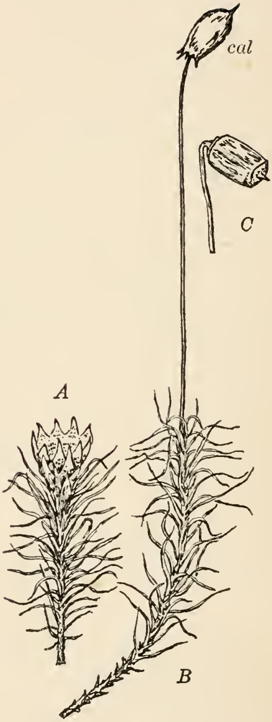

Fig. 265. A common moss (*Polytrichum commune*)

A, male plant, showing cup-like tip containing the antheridia. *B*, female plant with the sporophyte: *cal*, cap, or calyptra, over the developing spore case. *C*, a mature spore case with the calyptra removed

(Fig. 265, *C*). The development of the asexual spores in the spore case ends the life history of the moss plant, which may be formulated as follows:

$$\textit{Gametophyte}\begin{pmatrix}\text{protonema and}\\ \text{leafy moss plant}\end{pmatrix}{<}^{\textit{sperm}}_{\textit{egg}}{>} - \textit{Sporophyte} - \textit{asexual spore} - \textit{Gametophyte}, \text{ etc.}$$

This in abbreviated form becomes

$$G{<}^{s}_{e}{>} - S - sp - G{<}^{s}_{e}{>} - S - sp - G, \text{ etc.}$$

This formula is identical with the general life-history formula presented for the bryophytes in Sec. 285, and it is clear that gametophyte and sporophyte alternate with one another.

295. The leafy moss plant. The leafy moss plant is, of course, the conspicuous part of the gametophyte phase of the life history. It consists of an upright stem, branching in some forms, with the leaves almost always distributed spirally. The symmetry of the plant is therefore radial instead of having an upper and a lower side (dorsiventral) as in the leafy liverworts. The leaves consist for the most part of simple plates of cells, which in some forms can become dry and still retain their vitality, freshening up with the next rain.[1] The moss plant is fastened to the earth by filaments of protonema (Fig. 263), which grow out from the base of the stem and form a dense network underneath the moss plants (Fig. 261). This protonema becomes brown with age and serves as a system of root-like filaments, or rhizoids, by which the moss plant obtains water from the soil. The growth of the stem normally ends with the production of a terminal group of sexual organs, both of which (antheridia and archegonia) are found on the same plant in some species and on different plants (male and female) in others. Male plants are generally smaller than the female ones

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[1] The cells of the moss leaf are excellent subjects for study and have been described in Sec. 195 and illustrated in Fig. 169.

and more easily distinguished (Fig. 265, *A*) because the orange or reddish-brown clusters of antheridia lie exposed at the tip of the stem and are sometimes surrounded by a circle or rosette of modified or colored leaves. Female plants are larger, and the archegonia are hidden by enveloping leaves, which must be picked off to expose these sexual organs. The antheridia (Fig. 266, *a*) and archegonia (Fig. 268, *A*) are sometimes numerous in the clusters and lie among hair-like structures (paraphyses).

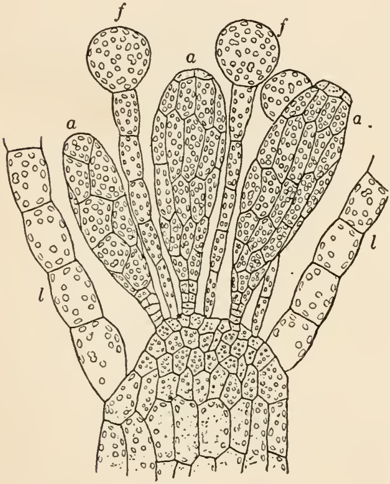

FIG. 266. Section through the tip of the male plant of a moss (*Funaria*)

a, antheridium; *f*, sterile filament, or paraphysis; *l*, leaf

FIG. 267. The antheridium of a common moss (*Funaria*)

a, antheridium; *b*, escaping sperms; *c*, a single sperm in its parent cell. — After Sachs

The mature antheridia and archegonia open only when wet by the swelling and separation of a group of cells at their tips. The sperms (Fig. 267, *b*) are discharged, then, after rains or heavy dews, so that the moss at that time is practically living an aquatic life. The archegonia (Fig. 268, *B*) have very long necks, and the relatively small egg lies at the bottom as in a flask. The sperms are attracted to the mouth of the open archegonium by substances in the mucilage within the neck, one of which at least is sugar. They swim down the neck to the egg, and one of them fertilizes it.

296. The sporophyte of the moss. The sporophytes of some of the common mosses are the most complex found among the bryophytes, with the possible exception of those of *Anthoceros.* There is generally a long stalk which bears a large spore case (Fig. 269, *A*). The structure of the spore case is very elaborate. A *cover* (operculum) is formed at the end, which falls off so that the spores may escape from within. In many mosses the cover is loosened and thrown off by an interesting mechanism, which is sometimes very highly developed. There may be a circle of cells with thickened and otherwise modified cell walls, forming a well-defined ring (Fig. 269, *A*, *r*) around the spore case underneath the cover. These cells change their form when wet, sometimes swelling greatly (Fig. 269, *C*), and thus loosen or tear the cover away from the spore case.

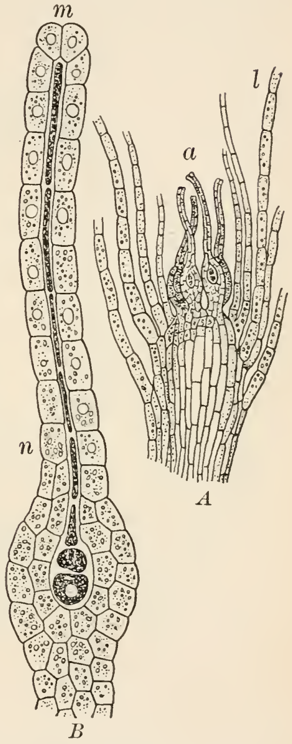

FIG. 268. Section through the tip of a female plant of a moss (*Funaria*)

A, group of archegonia *a*: *l*, leaf. *B*, an archegonium in detail, showing enlarged basal portion *e* with the egg, and the neck *n* above with its row of canal cells: *m*, mouth. — After Sachs

The rim of the opening formed when the cover falls off is surrounded by a circle of pointed triangular structures called *teeth* (Fig. 269, *B*, *t*), which meet at the center of the opening when folded inwards. The number of teeth is fixed for different mosses. Under the circle of teeth various mosses have another circle of much more delicate segments (Fig. 269, *B*, *s*) of the same number and general form. The teeth are sensitive to moisture, curling inwards and outwards with changes in the amount of vapor in the air, and by these movements they probably help in some types to empty the case of its spores, retaining them in wet weather and letting them fall out in dry.

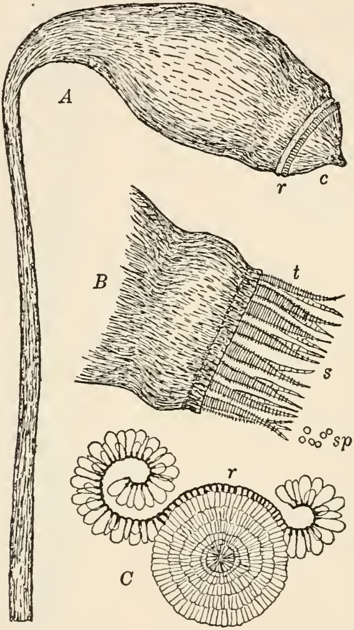

Fig. 269. The spore case of a common moss (*Bryum*)

A, the closed spore case: *c*, the cover (operculum); *r*, the ring. *B*, the rim of an open spore case, showing the outer circle of teeth *t*, inside of which is indicated the inner circle of delicate segments *s*: *sp*, spores. *C*, the cover after remaining for a minute in water: the cells of the ring *r* have absorbed the water and have swollen so that the ring has broken and curled backwards on two sides

The lower portion of the spore case has stomata (Fig. 270, *D*), and there is much chlorophyll-bearing tissue in the moss fruit that is capable of doing the work of photosynthesis just as in *Anthoceros.* But this sporophyte is, of course, dependent upon the gametophyte for its supply of water, which is taken up through the pointed foot of the stalk that is deeply sunken in the top of the leafy moss plant (Fig. 264, *B*). The spores are developed in groups of four (tetrads) within spore mother cells (Fig. 270, *F*, *sp*), which form a barrel-shaped tissue (Fig. 270, *E*, *sp*) within the spore case.

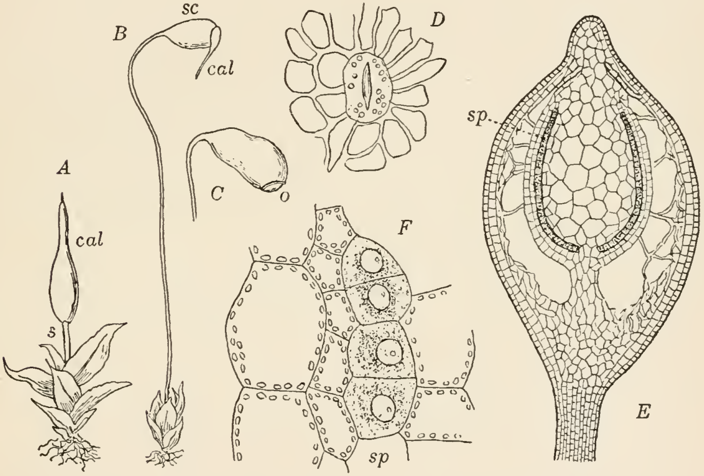

FIG. 270. The sporophyte of a common moss (*Funaria*)

A, young sporophyte *s* attached to the leafy moss plant and covered by the calyptra *cal*. *B*, sporophyte with mature spore case *sc* and calyptra *cal* at the tip. *C*, spore case with calyptra removed: *o*, the cover (operculum). *D*, a stoma from the surface of the spore case. *E*, section of young spore case, showing the cylindrical central region of spore-producing tissue *sp*. *F*, the spore-producing tissue in detail. — Adapted after Campbell

In spite of the immense numbers of species in the *Bryales,* the order is clearly separated from other groups of bryophytes as a side line of plant evolution, and its families and genera are distinguished by relatively minor differences.

THE ORIGIN AND EVOLUTION OF THE BRYOPHYTES

297. The origin of the bryophytes. The origin of the bryophytes is a mystery. They have of course arisen from the algæ, but there are no living algæ that resemble the bryophytes at all closely. *Coleochæte* [1] and the stoneworts (*Charales*) are the types most frequently considered in relation to the mosses. But the sexual organs of *Coleochæte* are one-celled, and the female organ of *Chara* bears only a superficial resemblance to an archegonium, while its antheridium is totally unlike any other male organ. There must have been formerly some group of the algæ, probably in the *Chlorophyceæ*, distinguished by having many-celled sexual organs from which the antheridium and archegonium of the bryophytes arose; for these complex sexual organs, together with the characteristic sporophyte generation, constitute the chief advance of the bryophytes over the algæ.

298. The evolution of the bryophytes. The evolution of the bryophytes is clearly related to the change from the aquatic habits of the algæ to the land habit. Living upon the land exposes the plant to the drying effects of the air and demands at once important structural adaptations, that is to say the plant must either develop a firm cell structure so that drying up will not injure the tissues seriously, or else it must maintain a constant connection with water through the surfaces of filaments (rhizoids) which are directly in contact with moisture. Many of the mosses and leafy liverworts have solved the problem in the first way and may become quite dry without serious injury. The *Riccia* and *Marchantia* forms and *Anthoceros*, on the other hand, are clearly adapted to the second alternative and die at once if removed from water or moist earth. The creeping habit and thallus structure of the simpler liverworts, while of advantage

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[1] The fructification of *Coleochæte* has frequently been compared to a simple type of sporophyte, somewhat like those found in the *Riccia* group of the liverworts. Recent investigations, however, indicate that this comparison is not justified, and that the fructification is not sporophytic at all. See Sec. 336 on the origin of the sporophyte.

in some situations, do not constitute so effective a plant body as a leafy stem with an erect habit, which secures a much greater exposure to air and light. Accordingly the appearance of leafy stems marked a great advance over the thallus structure. This new form of bryophyte plant body reached its highest development when the stem became erect with the leaves arranged spirally, as in the mosses, so as to give a radial symmetry.

It is quite safe to say that the adoption of the land habit was the chief cause of the rapid advance of the bryophytes over the algæ. The advance in vegetative structure is generally most marked in the gametophyte phase of the life history, although the sporophytes of such types as *Anthoceros* and certain mosses are clearly higher than the gametophytes. It may be noted in this connection that the next great forward step in the evolution of plants came in the fern group, or pteridophytes, when the sporophyte generation adopted the land habit and became independent of the gametophyte. However, this subject will be taken up in the next chapter.

SUMMARY OF THE BRYOPHYTES AND THALLOPHYTES

299. Bryophytes and thallophytes compared. It is possible at this point to make clear the fundamental reasons for the separation of the spore plants, so far studied, into the two great divisions of the plant kingdom called the *Thallophyta* and *Bryophyta.* It will be seen that the bryophytes have a set of very clearly defined characters, while the thallophytes are distinguished largely by the absence of these.

300. Summary of the bryophytes. The sexual organs are *many-celled* structures differentiated into female organs (archegonia) and male organs (antheridia). The fertilized egg develops at once into an *asexual* generation, or sporophyte, which produces *asexual spores* in groups of four, or *tetrads,* within certain cells called *spore mother cells.* The sporophyte, often called the fruit, alternates with the sexual generation, or gametophyte, and is always attached to it and dependent upon it for water and, at least in large part, for certain foods. The asexual spores produced by the sporophyte are of a new type not found in the thallophytes.

Class I. The liverworts, or Hepaticæ. This class is characterized by relatively simple sporophytes (*Anthoceros* excepted). The gametophytes are thalloid except in the leafy liverworts, and have distinct upper and lower surfaces (dorsiventral symmetry).

Class II. The mosses, or Musci. These have relatively complex sporophytes, whose spore cases open by covers, and the rim of the spore case is frequently fringed by a circle of teeth. The gametophytes have erect leafy stems, and the leaves are generally arranged spirally (radial symmetry).

301. Summary of the thallophytes. The sexual organs are almost always *one-celled* structures. The chief exceptions are the so-called plurilocular sporangia of the brown algæ (Sec. 235) and the peculiar antheridium of the stoneworts (Sec. 230). There is no organ in the thallophytes resembling the archegonium in structure or development. There is no alternation of sexual generations with asexual in most of the thallophytes. However, in the red algæ (*Rhodophyceæ*) and the sac fungi (*Ascomycetes*) the fertilized female cell produces peculiar fructifications called cystocarps and ascocarps, which develop asexual spores and constitute phases in the life history, alternating with the sexual plants. These phases are sporophytes, and there is a true alternation of generations in the red algæ and sac fungi, but these structures are peculiar and are believed to be independent developments in these two remarkable groups and not related to the sporophytes of the bryophytes. None of the thallophytes have sexual plants resembling in detail those of the liverworts or mosses. The plant body is generally a thallus, though the variety of form is very great, but the highest types in the brown and red algæ are differentiated into stems, leaf-like structures, and holdfasts. The cell structure of the thallophytes is generally much simpler than that in the plant bodies of the bryophytes, which owe their complexities of cell structure chiefly to the varied conditions introduced by the land habit; for the land habit requires the plant to protect itself from drying up, in the air. This, in general, means that a land plant must obtain water from the soil through some kind of organs adapted for that purpose (rhizoids or roots). And, as a rule, a land plant soon differentiates a protective layer of cells (epidermis), which helps to hold the water within its tissues. These structures are either entirely absent or present in greatly reduced form in aquatic plants, and for these reasons the cell structure of the aquatic thallophytes is generally very much simpler than that of the bryophytes.

Nevertheless, the thallophytes have developed some complicated organs with highly differentiated tissues, as in the kelps, rockweeds, red algæ, sac fungi, and the higher basidia fungi, such as the toadstools and mushrooms, puffballs, nest fungi, and carrion fungi. These complexities are, however, very special in character and not related to the structure of higher groups of plants.

CHAPTER XXV

THE PTERIDOPHYTES AND THE APPEARANCE OF HETEROSPORY

302. The pteridophytes.* The division *Pteridophyta* (meaning fern plants) comprises three classes: (1) the ferns, or *Filicineæ*, (2) the horsetails, or *Equisetineæ*, and (3) the club mosses, or *Lycopodineæ*. Representatives of these groups are generally somewhat familiar to all, and no one would think of grouping them with the liverworts and mosses. The differences become more conspicuous after a study of the life histories of pteridophytes, which shows that the large fern plant with its roots, stem, and leaves is really an asexual generation, or sporophyte, and that the gametophyte is represented by a small, comparatively insignificant sexual generation. This condition, so different from anything in the bryophytes and thallophytes, marks one of the great forward steps in the progress of plant evolution. It leads towards the seed plants, for these highest forms with their varied and complex structures are sporophytes, whose gametophyte generations are so much reduced that they can only be recognized by careful study of the processes of seed formation.

303. The advances in plant evolution up to the pteridophytes. It is well to summarize at this point the contributions of the thallophytes and bryophytes to the progress of plant evolution.

1. *The algæ.* The chief contributions of the algæ to plant evolution were four in number: (1) the attached many-celled plant body arose from the single-celled condition of the lowest

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* To the Instructor: The introduction to this chapter assumes that the life history of some fern has been studied in the laboratory.

algæ and soon became established as the vegetative period in the plant's life history; (2) as a result of this, the motile stages (zoöspores) became set apart as reproductive phases in the life histories, such reproductive motile stages, with other reproductive cells, being called spores; (3) certain of the reproductive cells became sexual in character, and these gametes at first similar (isogamy) were later differentiated into eggs and sperms (heterogamy); (4) alternation of generations developed in the red algæ and sac fungi, but probably independently of the same phenomenon in the bryophytes.

2. *The fungi.* The fungi as special and peculiar offshoots from the algæ have of course contributed nothing to the main evolutionary line running up to the higher plants.

3. *The liverworts and mosses.* The chief advances of the liverworts and mosses over the algæ were three in number: (1) many-celled sexual organs (antheridia and archegonia) took the place of the one-celled reproductive organs of the algæ; (2) an alternation of generations (gametophyte with sporophyte) became well established, together with the origin of a new type of asexual spore developed in groups of four (tetrads) by the sporophyte; (3) there was a general advance in the cell structure of the plant bodies because of adaptations to the more complex conditions of the land habit.

The sporophyte of the bryophytes is always attached to the gametophyte, and except in *Anthoceros* and some mosses it is not as complex as the gametophyte. In the pteridophytes, however, the conditions are reversed. The sporophyte is the large, conspicuous phase in the life history, and as it develops it becomes entirely independent of the gametophyte, while the latter appears relatively insignificant, although it holds, of course, a necessary place in the life history. The appearance in the pteridophytes of the sporophyte as an independent plant was the most important advance in plant evolution at this time, for the vegetative activities gradually became shifted, at first chiefly and finally wholly, from the sexual to the asexual generation.

Fig. 271. A fern (*Aspidium Filix-mas*)

A, part of the creeping stem, or rootstock, and fronds: *fr*, young fronds unrolling. *B*, under side of a frond, showing sori *s*. *C*, section through a sorus at right angles to surface of the leaf, showing indusium *i* and sporangia *s*. *D*, a sporangium discharging spores. — After Wossidlo

The material of this chapter will be treated under the following headings:

Class I. The ferns, or *Filicineæ*.
Class II. The horsetails, or *Equisetineæ*.
Class III. The club mosses, or *Lycopodineæ*.
Fossil plants and coal.
The origin and evolution of the pteridophytes.
Summary of the pteridophytes and their advances over the bryophytes.

CLASS I. THE FERNS, OR *FILICINEÆ*

304. The ferns. The ferns are a very large assemblage of more than four thousand species, and most of them can be recognized at a glance by the characteristic forms of their leaves, called *fronds*, and by their habits of growth. They are widely distributed, but reach their greatest luxuriance in the tropics, where they present some very striking displays. Thus the tree ferns have stems thirty or forty feet high, with a crown of fronds often fifteen or more feet in length. The stems of some of the tree ferns are covered by a sheath of fibrous roots (as in Dicksonia, Plate VII), and in other types the bases of the old and withered fronds form a similar investment. There are also in the tropics certain small delicate ferns

FIG. 272. The stag-horn fern (*Platycerium Willinki*)

A tropical epiphytic fern with two forms of leaves, one of which grows closely against the bark of trees and gathers and holds moisture and humus. — After Goebel called filmy ferns, whose stems and fronds are as delicate as mosses. Some peculiar types, as the stag-horn fern (*Platycerium*, Figs. 272, 364), grow over the surface of tropical trees and are consequently called *epiphytes* (meaning upon a plant). These have certain flattened leaves (Fig. 272) closely pressed against the surface to which the plants are attached, where they gather and hold moisture and humus. The roots of the filmy ferns and the epiphytes are very poorly developed, or entirely wanting, but the air of a tropical forest is so saturated with water that they obtain all that they need from the dripping moisture and wet surfaces upon which they grow.

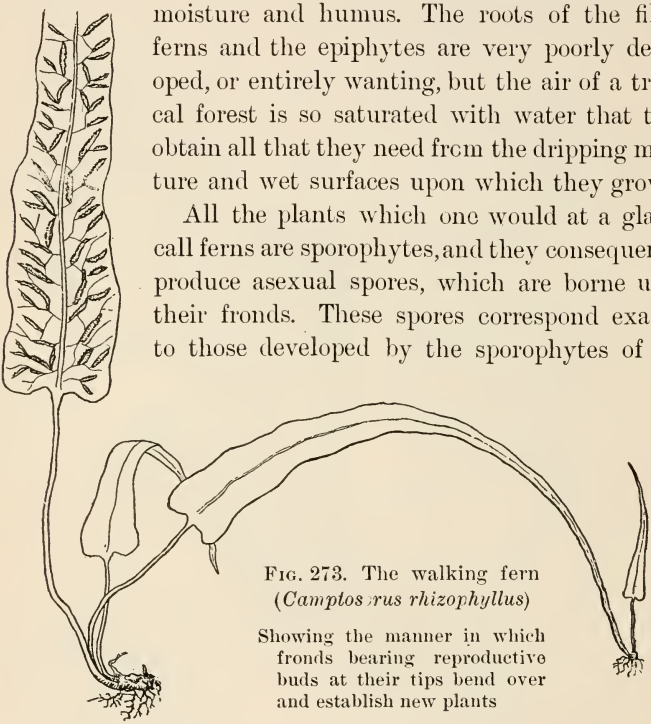

Fig. 273. The walking fern (*Camptosorus rhizophyllus*)

Showing the manner in which fronds bearing reproductive buds at their tips bend over and establish new plants

All the plants which one would at a glance call ferns are sporophytes, and they consequently produce asexual spores, which are borne upon their fronds. These spores correspond exactly to those developed by the sporophytes of the liverworts and mosses, and they give rise to a small sexual generation, the gametophyte. The life history of a pteridophyte can be most easily studied from one of the common ferns familiar to us in the woods, greenhouses, and gardens.[1]

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[1] The moonwort and adder's-tongue (Sec. 315) illustrate more primitive conditions in the pteridophytes than the common ferns, but are not generally available for type studies.

PLATE VII. Tree ferns (*Dicksonia antarctica*) from Tasmania

These tree ferns grow to be 30 to 40 feet high, with fronds 8 to 12 feet long, and the trunks, densely covered with small roots, may become 3 feet thick. — After a photograph in the Harvard Museum

305. The common ferns. The common ferns (order *Filicales*) completely outclass all other orders of pteridophytes in number of species and mass of vegetation. The forms are exceedingly various. The stems may be short and close to the ground, or upright trunks, as in the tree ferns. But many types have creeping stems, frequently wholly buried in the earth as underground stems, or rootstocks, well illustrated by the common brake, or bracken fern (*Pteris aquilina*). Some ferns have peculiar methods of reproduction by buds that are formed on the leaves, as in the bladder fern (*Cystopteris bulbifera*), or the walking fern (*Camptosorus*) shown in Fig. 273.

The fronds or leaves arise from the tip of the stem and form clusters or crowns around the top of upright structures, but are generally somewhat scattered along the creeping stems. Most fronds are much cut or divided (compound) after regular and various patterns (Fig. 271). They are developed very slowly in some genera, remaining rolled up in the bud for several months. However, when fully formed and in the proper season they unroll comparatively quickly from the base in a very characteristic manner until the apex finally appears above.

The cell structure of the leaves, stems, and roots is very much more complex than the cell structure in the bryophytes and recalls at once the tissues of the seed plants (see Part I, Chapters VII and XII). The plant body has a system of tissues, called *fibro-vascular bundles* (Fig. 274), whose parts are much modified for two important functions. One tissue is composed of large cells (Fig. 274, *t*) empty of protoplasm and with heavy thickened walls marked with curious pits. These elements, called *tracheids*, compose the *woody* part of the fibro-vascular bundle termed the *xylem*, and their purpose is to conduct water from the roots to parts of the plant above ground. But they are also very important for the strength that they give to stems and leaves. Another tissue is composed chiefly of cells, called *sieve tubes* (Fig. 274, *st*), which contain much protoplasm and food material and make up a softer region of the bundle termed *bast* or *phloëm.* The bast regions are known to be paths for the distribution of food material in the plant. The structure of the fern frond is essentially similar to that of the leaf of a seed plant. There are *stomata* on the lower surface and chlorophyll-bearing tissues underneath the outer cell membrane, or *epidermis.* The fibro-vascular bundles run out into the green expanded portions of the leaves as forking veins, which do not, however, generally unite to form the close network so characteristic of dicotyledonous seed plants.

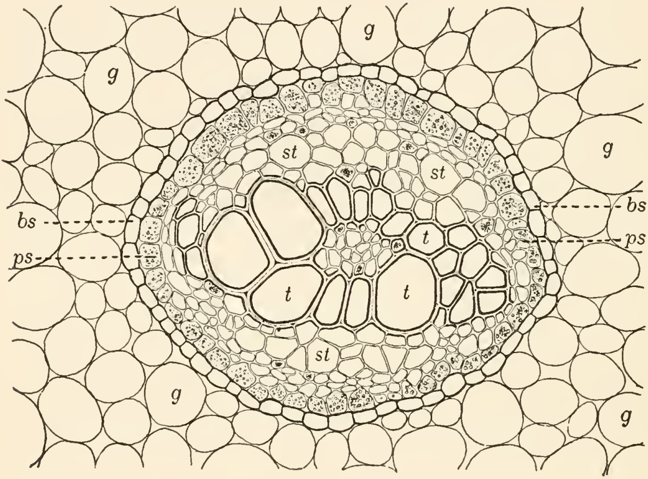

Fig. 274. Fibro-vascular bundle from the underground stem, or rootstock, of the common brake (*Pteris aquilina*)

g, ground tissue, or parenchyma; *bs*, bundle sheath; *ps*, bast, or phloëm, sheath surrounding the sieve tubes (*st*) and bast fibers which compose the bast, or phloëm; *t*, large, thick-walled cells called tracheids, which with smaller cells in the center make up the wood, or xylem

As stated above, the fibro-vascular bundles greatly strengthen the tissues of the leaves and stems, for they form a sort of skeleton in the plant. They are frequently assisted in their strengthening functions, especially in the stem, by regions of *rigid tissue*, which may be variously situated, sometimes under the epidermis and sometimes forming broad strands in the interior. This rigid tissue (sclerenchyma) is composed of elongated cells with very heavy, much-thickened walls, which are often yellowish in color. This tissue is developed from the thin-walled cells (parenchyma), called the *ground tissue,* that compose the greater part of the interior of the stems.

306. Spore formation. The sporophyte nature of the fern plant becomes clear at the time of fructification. Certain ones or sometimes all of the fern fronds as they grow older develop spore cases, or *sporangia.* These are variously situated on the fronds, sometimes appearing as clusters or spots, called *sori* (singular, *sorus,* meaning a heap), on the under surface and sometimes in lines along the under edge. A sorus may be naked, but it is frequently protected by a membranous outgrowth, or *indusium,* from the surface of the frond (Fig. 271, *C*, *i*).

The sporangia are stalked and somewhat flattened many-celled cases, each of which develops from a single surface cell of the frond. There are sixteen spore mother cells in the interior of the spore case, each of which gives rise to a group of four spores (tetrad). The method of spore formation, four spores in each mother cell, is thus identical with that of the bryophytes.

The sporangium of many common ferns is composed of thin-walled cells except along the edge, where there is a line with much-thickened walls, which extends from the stalk about two thirds around on the outside (Fig. 275, *A*). This line of cells is called the *ring,* and as the sporangium ripens and becomes dry, the ring is forcibly held like a bent spring. Finally, the delicate cells at the side of the spore case opposite the ring are unable to stand the strain and are torn apart so that the ring straightens somewhat and a wide rent is made in the side of the sporangium (Fig. 275, *B*, *C*). The spores are thrown out violently through the rent for a considerable distance. This is the structure of the spore case in the family *Polypodiaceæ,* for the several families of the *Filicales* have sporangia which differ from one another in form and in the structure and position of the ring.

307. Fronds, vegetative leaves, and spore leaves (sporophylls). Most fronds are vegetative, that is, perform chlorophyll work (photosynthesis) during the early part of the season and develop sporangia later. However, some types, as the royal and cinnamon ferns (*Osmunda*) and the sensitive and ostrich ferns (*Onoclea*), devote the whole of certain leaves or portions of them entirely to the work of spore production. The blades of these fronds or portions of fronds never become expanded, but remain somewhat rolled up, forming pod-like structures in which the sporangia are developed (Fig. 276). Other fronds on these ferns are devoted entirely to vegetative activities and never develop sporangia. There is thus in some ferns a division of labor among the fronds, certain of them becoming strictly *vegetative leaves*, while others are spore leaves, called *sporophylls*.

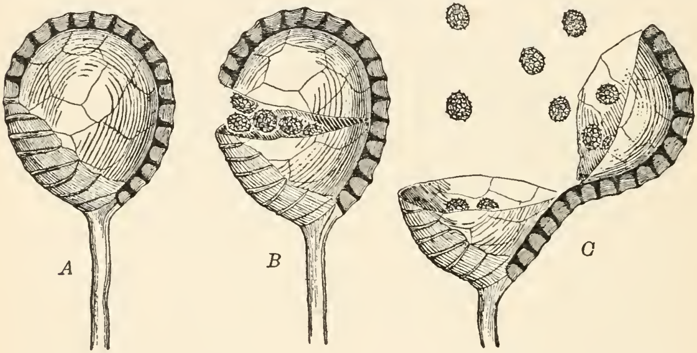

FIG. 275. The sporangium of a common fern (*Aspidium Filix-mas*)

A, closed sporangium; *B*, sporangium opening; *C*, fully opened and discharging the spores. — After Kerner

There is a constant tendency in the pteridophytes to give all the work of spore production to the specialized spore leaves (sporophylls), which means that all the other fronds on the plant become entirely devoted to vegetative activities and may then be called vegetative leaves or simply *leaves* in the sense in which this term is generally used in the seed plants. This differentiation of the frond into leaves and sporophylls reaches a high point of development in the horsetails and club mosses, and becomes even more conspicuous in the seed plants, as will appear later.

308. The gametophyte of the fern. The fern spore germinates readily on moist surfaces and puts forth a delicate filament, consisting of a row of cells (Fig. 277, *A*). Several oblique cell walls at the end of this filament cut out a triangular apical cell (Fig. 277, *B*, *x*), which becomes the growing point. The final development is usually a small, delicate, heart-shaped, thallus-like body resembling a small liverwort, but only one cell in thickness, except in the middle region. The apical cell (Fig. 277, *C*, *x*) generally becomes situated in a deep notch at the forward end (Fig. 277, *D*) because of the greater cell growth on either side. The back part of the structure becomes fastened to the earth by numerous delicate filaments or rhizoids which act like root hairs. This structure develops the sexual organs of the fern and is consequently the gametophyte generation in the life history. It is called the *prothallium* because it precedes the fern plant (sporophyte).

FIG. 276. The sensitive fern (*Onoclea sensibilis*)

Showing vegetative leaf and spore leaf (sporophyll) rising from the creeping rootstock

Both sexual organs (antheridia and archegonia) are found on the same prothallium if it is well developed. But when prothallia are crowded or grown under other unfavorable conditions they remain small and stunted and become irregular in form (Fig. 278, *A*). Such dwarf gametophytes only develop antheridia.

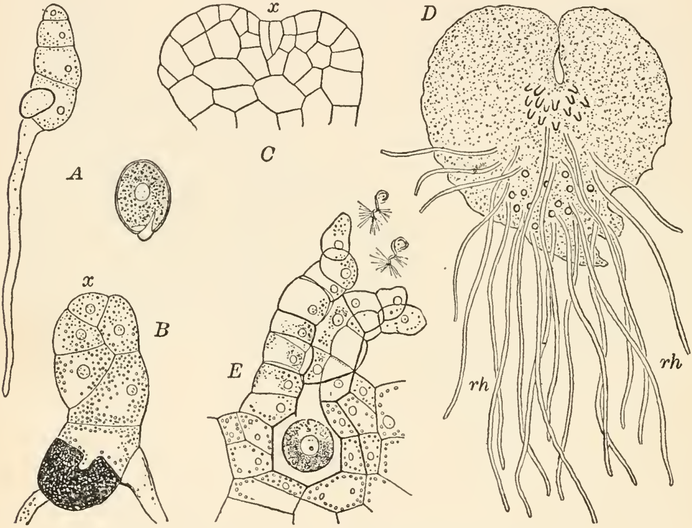

FIG. 277. The fern prothallium and archegonium

A, stages in the germination of the spore. *B*, young prothallium, showing first appearance of wedged-shaped, apical cell *x*. *C*, tip of prothallium beginning to take on the heart-shaped form: *x*, apical cell. *D*, mature prothallium, showing group of archegonia on the cushion just back of the notch, and antheridia further back: *rh*, rhizoids. *E*, an open archegonium with egg ready for fertilization, and two sperms near the entrance of the neck. — *A*, *B*, *C*, *E*, after Campbell; *D*, after Schenck

On well-nourished prothallia the antheridia are formed first on the edge and lower surface of the back portions. The archegonia are developed last when the prothallium is quite large, and are only found on the thickened region, called the *cushion*, directly back of the notch, or growing point.

The antheridia. The antheridia (Fig. 278, *B*, *C*) are very much smaller than those of the bryophytes. They develop from a single cell which projects above the surface of the prothallus. There are only three cells forming the capsule of this structure, — a cover cell above, a ring-shaped cell in the middle, and a funnel-shaped, basal cell. These three cells inclose at first a large central protoplast, from which is developed a group of one hundred or more small cubical cells that produce the sperms, as in the bryophytes. These sperms are, however, very different in form from the two-ciliate sperms of the liverworts and mosses and many algæ. Each consists of a spirally coiled band (Fig. 278, *D*), whose narrower-pointed end is covered with numerous cilia, making it a many-ciliate sperm.

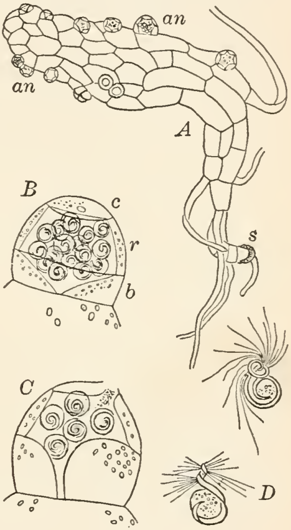

FIG. 278. The antheridium and sperms of a fern (*Onoclea*)

A, small prothallium with many antheridia *an*: *s*, old spore wall. *B*, antheridium, showing cover cell *c*, ring cell *r*, and basal cell *b*, inclosing the sperm mother cells. *C*, antheridium opening. *D*, sperms. — After Campbell

The archegonia. The archegonia of the ferns are also much smaller than those of the bryophytes and simpler in structure. The short neck alone projects above the surface of the prothallus (Fig. 277, *E*) and generally bends backward, probably because the forward part of the prothallium is not directly on the earth, but rises at an angle. The egg lies beneath the surface of the prothallium, so that the base of the archegonium may be described as sunken. There are only two or three canal cells (Sec. 283) in this archegonium.

The eggs are fertilized under exactly the same conditions as in the bryophytes (Sec. 283). When the prothallia are wet the sexual organs open, and the sperms swim over the moist surfaces and are attracted to the necks of the archegonia by substances secreted within, one of which at least is malic acid. The sperms swim down the neck to the egg, and one of them fertilizes it. The fern plant then, like the liverwort and moss, practically returns to the aquatic life of the algæ at the time when the sexual cells are functional.

309. The development of the sporophyte. The early stages in the development of the fern sporophyte as in the bryophytes are passed entirely within the tissue of the prothallium, surrounded by the remains of the archegonium. The fertilized egg cell divides, and there are formed four regions in the embryo fern: (1) a stem region, (2) the first leaf, (3) the first root, and (4) an organ of attachment to the gametophyte called the *foot.* The leaf and root soon break out of the archegonium, the first growing upward and the second into the earth (Fig. 279, *A*, *B*). The stem grows more slowly. The young fern all this time obtains nourishment from the prothallium through the foot after exactly the same method as in the bryophytes. However, when

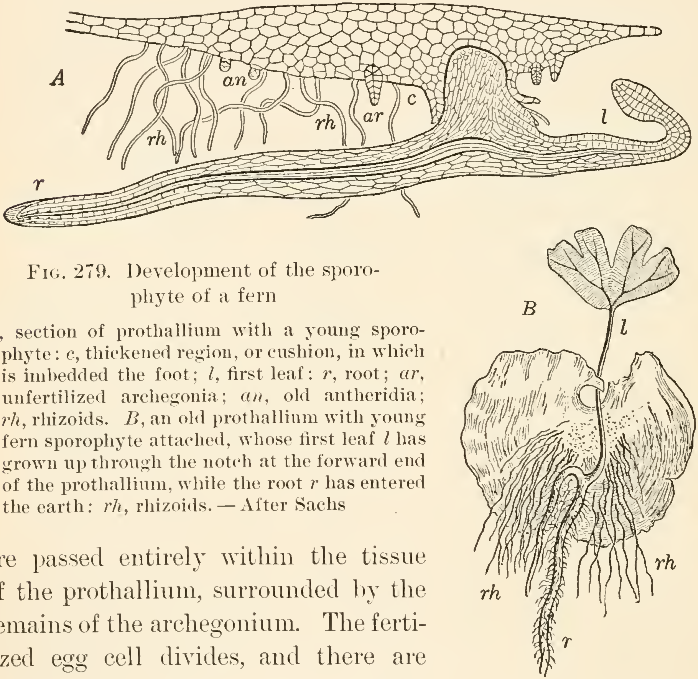

Fig. 279. Development of the sporophyte of a fern

A, section of prothallium with a young sporophyte: *c*, thickened region, or cushion, in which is imbedded the foot; *l*, first leaf: *r*, root; *ar*, unfertilized archegonia; *an*, old antheridia; *rh*, rhizoids. *B*, an old prothallium with young fern sporophyte attached, whose first leaf *l* has grown up through the notch at the forward end of the prothallium, while the root *r* has entered the earth: *rh*, rhizoids. — After Sachs the root and leaf are well established the sporophyte becomes independent of the gametophyte, which gradually dies within a few weeks or months. It is the development of root, stem, and leaf on the part of the sporophyte, giving it complete independence, which marks the greatest advance of the pteridophytes over the bryophytes.

310. Summary of the life history of a fern. The alternation of generations in the fern is much more apparent than in the liverworts and mosses because both gametophyte and sporophyte are independent plants. The two groups (bryophytes and pteridophytes) are in striking contrast in the relative importance of the two generations. The gametophytes of the bryophytes are relatively large, long-lived, and complex organisms (with stems and leaves in the mosses and leafy liverworts), while the sporophytes are simple and so dependent upon the gametophyte that they were for many years called its fruit. The gametophytes of the pteridophytes, on the contrary, are small, short-lived, and simple, while the sporophytes are very large and complex (possessing stem, roots, leaves, and a vascular system) and, except in their earliest stages of development, completely independent of the gametophytes.

The life history of a fern may be formulated as follows:

$$\textit{Gametophyte}\,(\text{prothallium}) < \begin{matrix}\textit{sperm}\\ \textit{egg}\end{matrix} > - \textit{Sporophyte}\,(\text{fern plant})$$

$$- \textit{asexual spores} - \textit{Gametophyte}, \text{ etc.}$$

This in abbreviated form becomes

$$G < \begin{matrix}s\\ e\end{matrix} > - S - sp - G < \begin{matrix}s\\ e\end{matrix} > - S - sp - G, \text{ etc.,}$$

and is the same life-history formula as that of the bryophytes (Sec. 285).

311. Apogamy and apospory in the ferns. There are some irregularities in the life histories of certain ferns which are not uncommon in greenhouses and under cultivation (species of *Pteris*, *Aspidium*, *Athyrium*, *Nephrodium*, etc.). Prothallia sometime fail to develop archegonia or the archegonia do not function, but the sporophyte generation arises as a bud-like outgrowth from the prothallium. In other cases the egg may develop without fertilization (parthenogenesis). Such suppressions of sexuality with the development of a succeeding generation *asexually* are called *apogamy.* The phenomenon has been noted before in the water molds (Sec. 262) and other fungi, and it is found in various groups throughout the plant kingdom.

Apospory is the suppression of the process of spore formation and the development of a gametophyte generation directly from the sporophyte. It is found in many of the ferns, which are also apogamous, and is shown by the presence of prothallia, which are direct outgrowths from the fern frond in the place of the sporangia, or sometimes at the tips. Apospory is also found in certain mosses where protonema may develop directly from portions of the stalk and spore cases of the sporophytes.

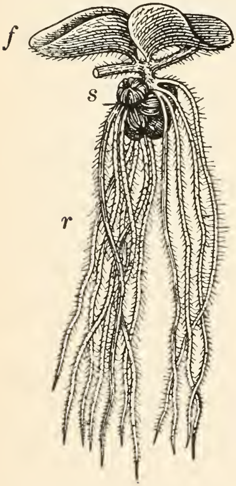

FIG. 280. A water fern (*Salvinia*)

f, floating leaves; *r*, highly modified leaf acting as a root; *s*, spore fruits. — After Pringsheim

Apogamy and apospory are both short cuts in the life histories, which are believed to be due to some unusual life conditions that interfere with the regular development of gametes and spores in the normal life histories, established during the evolution of plant groups.

312. The water ferns. The water ferns (order *Hydropterales*) include four interesting genera (*Marsilia*, *Pilularia*, *Salvinia*, and *Azolla*), each of which is remarkable for some peculiarity of structure. *Salvinia* (Fig. 280) and *Azolla* are floating aquatics, and *Marsilia* and *Pilularia* are either aquatic or grow in very wet places. These habits give the common name of water ferns to the group. They are important illustrations of the condition called *heterospory,* which is briefly described in Sec. 214 and discussed in some detail in Chapter XXVII. The *Hydropterales* are believed to have been derived from the *Filicales*, and the development of heterospory is the most important advance over that group. We can only consider the rather widely distributed type *Marsilia*.

313. Marsilia.* *Marsilia*, the clover leaf fern, or pepperwort, is easily recognized from the form of the leaf (Fig. 281, *A*). The leaves arise from a creeping stem which in certain species, as *M. quadrifolia*, grow over the mud in shallow water along the margins of ponds and streams, but often come out of the water upon muddy banks. Other species, as *M. vestita*, grow almost entirely on muddy banks or in wet meadows.

The spores of *Marsilia* are developed in bean-shaped

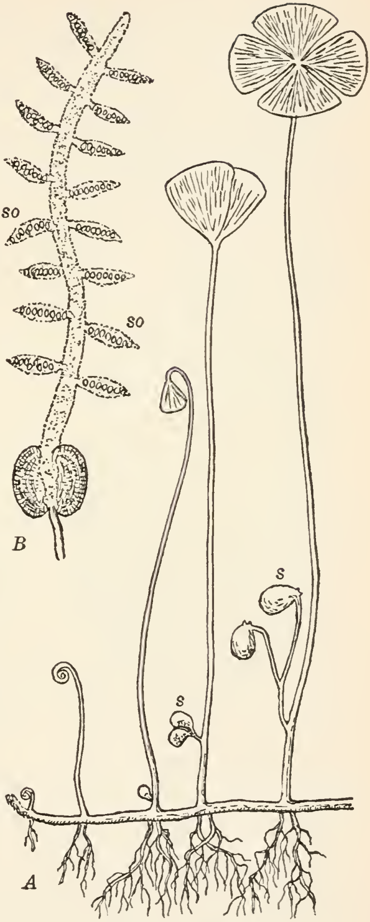

FIG. 281. *Marsilia*

A, creeping stem of *Marsilia quadrifolia*, showing a series of leaves in various stages of development: *s*, spore fruits (sporocarps). *B*, a spore fruit of *M. vestita*, which has opened in water and extruded a gelatinous, worm-like structure bearing sori *so*

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* TO THE INSTRUCTOR: If only one heterosporous pteridophyte can be studied in the laboratory, it is much better that the type be *Selaginella*. For this reason the account of *Marsilia* has been made short. The life-history formula is, of course, the same as that of *Selaginella*, which is fully treated in Sec. 326.

spore fruits, or sporocarps, borne in groups on short stalks. These spore fruits (Fig. 281, *A*, *s*) are really modified portions of leaves, which are excellent illustrations of very highly developed sporophylls, much more specialized than the spore leaves of such ferns as *Onoelea* and *Osmunda.*

The spore fruits burst open when soaked in water through the swelling of mucilage within, and the contents come out as a gelatinous, worm-like structure bearing large groups (sori) of spores along the sides (Fig. 281, *B*, *so*). The spores are developed in essentially the same manner as in the common ferns (*Filicales*), but the tissues of the sporangia are so much modified that the resemblances can only be followed through a detailed developmental study. The spores are set free by the softening of the gelatinous material, and they begin to germinate at once in the water. They are of two sizes, large and small, and are consequently called *megaspores* and *microspores.* This condition is termed *heterospory.*

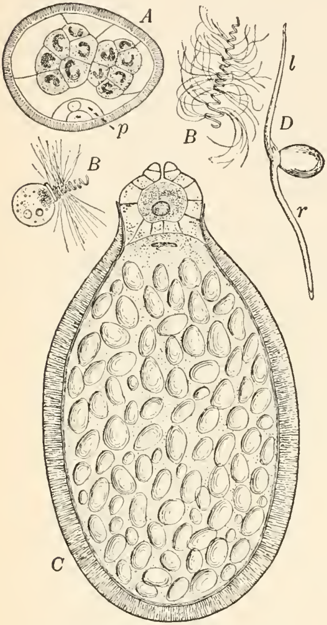

FIG. 282. Gametophytes of *Marsilia vestita*

A, male gametophyte within microspore: *p*, prothallial cells; two groups of sperm mother cells shown within. *B*, sperms. *C*, female gametophyte consisting of a single archegonium at one end of the megaspore, which is filled with starch grains. *D*, a week-old embryo (slightly magnified) still attached to the megaspore: *l*, first leaf; *r*, root. — *A*, *B*, after Campbell

The megaspores are full of starch grains, which furnish the food for the development in a few hours of a small female gametophyte. This gametophyte (Fig. 282, *C*) consists of a single archegonium at one end of the spore. Although the cells are somewhat greenish, it is perfectly clear that the food of this much-reduced prothallium is furnished chiefly by the sporophyte by means of the megaspore. The gametophyte of *Marsilia* has therefore degenerated from the independent condition in the common ferns and is now no longer self-supporting, but is dependent upon food stored by the sporophyte, a relation which is exactly the reverse of that in the bryophytes.

The microspore develops a very small male gametophyte even more quickly than the megaspore develops the female one. This structure consists of a lens-shaped sterile cell called the *prothallial cell* (Fig. 282, *A*, *p*), together with a group of cells which probably represent a single much-reduced antheridium. The sperms are formed within this group. They are remarkably long, coiled bands covered with cilia (Fig. 282, *B*), and are among the largest sperms in the pteridophytes.

The young sporophyte develops within the archegonium, following essentially the same history as that of the common ferns, and is consequently attached to the megaspore (Fig. 282, *D*). But there is an important peculiarity in its relation to food supply. This sporophyte makes use of considerable food that remains in the megaspore after the development of the female gametophyte. The *Marsilia* plant, therefore, actually provides for the next sporophyte generation by storing food in the megaspore. This provision is strikingly similar, as will appear later, to the conditions in the seed where the embryo (young sporophyte) is nourished by food stored in the seed by the sporophyte of the preceding generation.

Marsilia illustrates exceptionally well three important principles in the evolution of pteridophytes and seed plants, namely: (1) the establishment of heterospory, resulting in the separation of male and female gametophytes, (2) the reduction or degeneration of the gametophytes, which become dependent upon food stored in the microspores and megaspores, and (3) provision in the megaspore for the nourishment of the embryo of the succeeding sporophyte generation.

314. Heterospory. *Heterospory* (meaning dissimilar spores) arose in the pteridophytes with the establishment of two sizes of spores, — megaspores and microspores. Pteridophytes having these are called *heterosporous,* and those with spores of the same size, as in the common ferns (*Filicales*), are called *homosporous* (meaning similar spores). With heterospory came also a differentiation of the gametophytes into male and female structures, the first developing from the microspores and the second developing from the megaspores.

315. The moonwort and adder's-tongue. The moonwort (*Botrychium*, Fig. 283, *A*) and the adder's-tongue (*Ophioglossum*, Fig. 283, *B*) are in the same group (order *Ophioglossales*) and illustrate certain primitive conditions in the pteridophytes. These forms do not have external sporangia, as in the *Filicales,* but the spores are developed in sunken regions along peculiar stalks. Such sunken sporangia are much more primitive in structure than those which develop upon the surface of the plant, for they resemble more closely the conditions in the bryophytes where the spore mother cells are found in the interior of the plant. The spore-bearing stalks are accompanied by sterile blades devoted to the vegetative activities, so that these leaves illustrate the same sort of division of labor as is found in the royal fern (*Osmunda regalis*). The gametophytes are underground, tuberous bodies generally, destitute of chlorophyll and

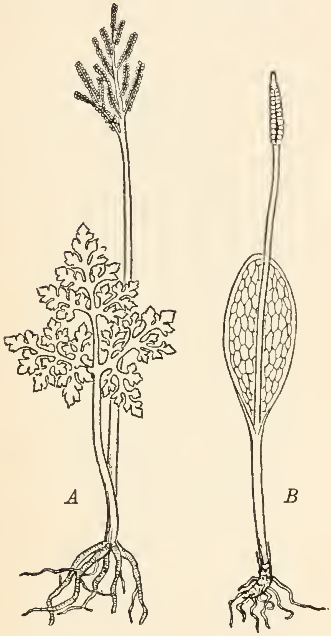

Fig. 283. The moonwort and adder's-tongue

A, the moonwort (*Botrychium ternatum*); *B*, the adder's-tongue (*Ophioglossum vulgatum*) saprophytic in their life habits, being associated with certain fungi which form a mycorrhizal partnership (Sec. 278) with them.

CLASS II. THE HORSETAILS, OR *EQUISETINEÆ*

316. The horsetails. The horsetails, or scouring rushes, are all comprised in the genus *Equisetum*, which contains about 40 living species, the sole modern representatives of the order *Equisetales* and the class *Equisetineæ*. These plants are the remnants of what was a very extensive flora in an early geological period, called the Carboniferous Age, when the largest deposits of coal were formed. The ancient relatives of *Equisetum* (Plate VIII, 2), together with the club mosses, were then trees and formed the forests in those times. The horsetails live now under what seem to be rather severe conditions in bare or sandy soils that are unfavorable for the growth of trees, herbs, and grasses. They illustrate very well the way in which an ancient group is sometimes able to avoid total extinction by withdrawing as far as possible from competition with the recent floras, and thus hold its own by means of peculiar life habits and adjustments to special conditions.

The most striking feature of the morphology of *Equisetum* is the total absence of foliage suitable for vegetative activities (photosynthesis). The foliage is represented by sheaths (Fig. 284, *A*, *B*), which are found at the joints of the hollow stem. The points on these sheaths are the tips of small leaves more or less united below. The vegetative functions are performed by the green stems. These are fluted, that is, they have numerous ridges which run lengthwise, and the depressions between the ridges contain stomata, which lie above the chlorophyll-bearing tissues (Fig. 284, *F*, *c*). The epidermis contains deposits of silica, which is the chief substance in glass, and consequently the stems feel rough. They are sometimes used for scouring or polishing metal; hence the origin of one of the common names, "scouring rush."

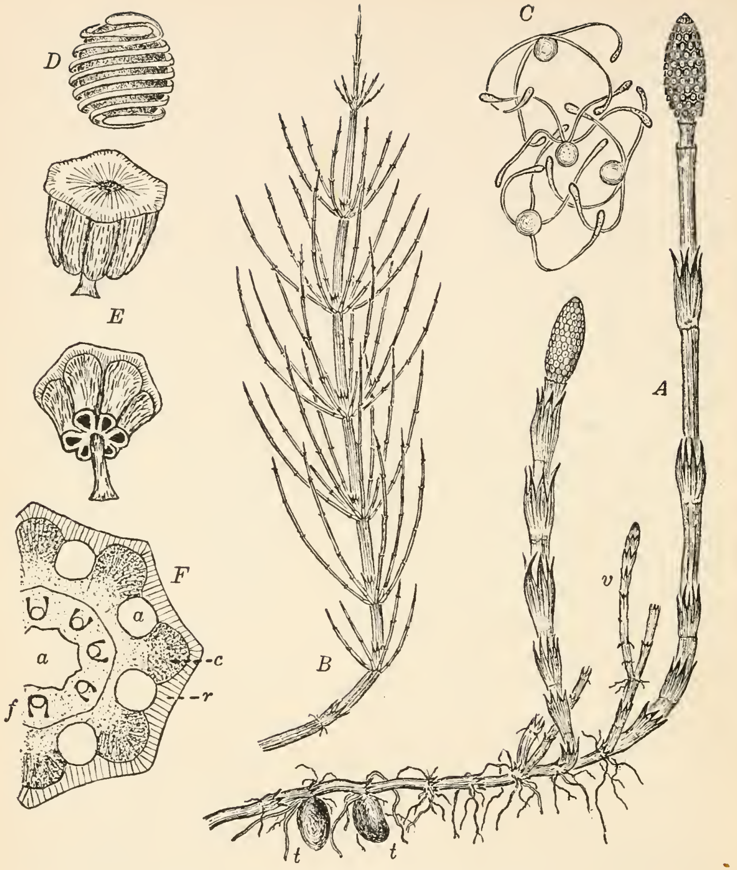

Fig. 284. A horsetail (*Equisetum arvense*)

A, fertile stems, bearing cones rising from the creeping rootstock: *t*, tuberous bodies; *v*, young vegetative stem below ground and ready to grow into the mature structure shown in *B*. *B*, vegetative stem as it appears perhaps three weeks after the fertile stems have shed their spores and died. *C*, a group of spores with their elaters expanded. *D*, a spore with the elaters coiled around it. *E*, two views of the spore leaves (sporophylls), showing the group of sporangia. *F*, portion of a section of the stem: *a*, air spaces; *c*, chlorophyll-bearing tissues; *r*, rigid outer tissues; *f*, fibro-vascular bundle around small air space. — *A*, *B*, *C*, *D*, after Schenck

The stems are generally of two forms. There are green *aërial* stems above ground, unbranched in some species, but quite bushy in others by the development of circles of side branches at the joints (Fig. 284, *B*). The aërial stems arise from creeping underground stems, or rootstocks, which have the same jointed structure and sheaths of degenerate leaves, but are not green and often not hollow. The underground stems live from year to year and grow rapidly through the soil, frequently establishing large beds of horsetails, as, for example, along railroad tracks and the margins of sandy pools and ponds.

The stem has large, central air cavities, running from joint to joint, and also a number of smaller air canals, alternating with the fibro-vascular bundles (Fig. 284, *F*, *a*). It is strengthened by thick-walled cells, forming a rigid tissue (Fig. 284, *F*, *r*) under the epidermis, and is consequently well protected from the danger of drying up. These peculiarities, together with the reduced leaf surface, are characters which the horsetails have in common with many desert plants (xerophytes), and they permit them to live when necessary under very severe drought conditions.

The fructification of *Equisetum* is a *cone* (Fig. 284, *A*) developed at the tip of the stem, and it is composed of scale-like spore leaves (sporophylls), which fit closely together and develop spores in sporangia upon their under surfaces (Fig. 284, *E*). These cones are generally found on ordinary green stems. However, in some species, as *E. arvense*, the stems which first appear above ground are pale in color and are devoted entirely to the development of the cones and die after the spores are shed, while the green vegetative stems appear later.

317. The cone of Equisetum. A cone, or *strobilus*, is a compact group of spore leaves (sporophylls) distributed around the tip of a stem and distinct from the rest of the plant. It takes its compact form because the sporophylls are closely set together and frequently so much modified that their structure is not apparent at a glance. Each sporophyll in *Equisetum* consists of a short stalk attached to the side of the stem and bearing an angled shield-shaped top (Fig. 284, *E*). A group of sporangia hang down all around the stalk from the lower surface of the shield, and each develops from a group of cells instead of from a single cell, as in the common ferns (*Filicales*). The shields separate from one another when the cone matures, and the ripe spores escape through rents in the sporangia and sift out between the shields. The spores are formed in groups of four (tetrads) in the spore mother cells.

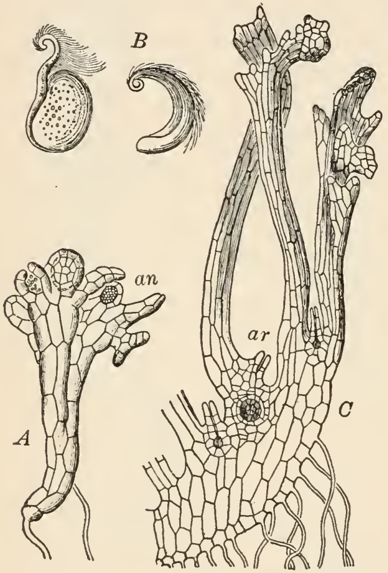

FIG. 285. Gametophytes of *Equisetum*
A, male prothallium: *an*, antheridium. *B*, sperms. *C*, female prothallium: *ar*, archegonium. — *A*, *C*, after Hofmeister; *B*, after Schacht

Each spore (Fig. 284, *C, D*) bears four filaments developed from an outer layer of the spore wall, which splits into bands that separate from one another, but remain attached to the spore at one point. The filaments coil around it when moist, but loosen and spread out when dry. These movements must assist the escape of the spores from the sporangia. The filaments also serve as wings in the distribution of the spores by the wind, and they become entangled with one another so that groups cling together and are carried away and germinate in clusters. The spores are of the same size, and therefore *Equisetum* is homosporous.

318. The gametophytes of Equisetum. The spores only retain their vitality for a few days. They produce green gametophytes somewhat like fern prothallia, but very irregular in form (Fig. 285, *A*, *C*), the larger with long lobes, at the bases of which are situated the sexual organs. The prothallia are normally diœcious, that is, male and female in sex, but since the spores are distributed in groups, antheridial plants are likely to develop in the same cluster with the archegonial. The sexual organs are sunken in the tissues of the gametophytes. The sperms are coiled, many-ciliate protoplasts (Fig. 285, *B*) resembling those of the common ferns.

The early stages in the development of the young *Equisetum* sporophyte from the fertilized egg are the same as those of the common ferns. This together with the similar gametophytes and sperms is believed to indicate a distant relationship between the *Equisetineæ* and *Filicineæ*, even though the mature sporophytes of the two groups appear so different in structure.

CLASS III. THE CLUB MOSSES, OR *LYCOPODINEÆ*

319. The club mosses. The *Lycopodineæ* take their common name of club mosses from the moss-like appearance of the stems, which in most forms are covered with small leaves (Figs. 286, 289, *A*), and the fructification, which is generally a club-shaped cone developed at the end of the stem (Figs. 287, *A*; 289, *A*). *Isoetes* (Fig. 291) is, however, in these particulars a conspicuous exception. But the club mosses are very much larger than any of the true mosses (*Musci*), and are of course sporophytes, like the horsetails and ferns, while the true mosses are gametophytes. Like the horsetails, they are the remnants of a very ancient group which formed forests in the Carboniferous Age (Plate VIII, 3, 4); also, they have been able to persist only by adapting themselves to life conditions where they do not encounter keen competition with grasses and herbs. Almost all of the *Lycopodineæ* are contained in three genera: *Lycopodium* (about 100 species), *Selaginella* (about 500 species), and *Isoetes* (some 60 species). But in addition there are several remarkable types (*Phylloglossum*, *Psilotum*, *Tmesipteris*) which are tropical or sub-tropical and cannot be described here.

320. Lycopodium. *Lycopodium* includes the larger club mosses, frequently called lycŏpods, and are distinguished by having needle-like leaves arranged spirally on the stem (Fig. 286) and similar spores (homosporous). The stems are of two forms: (1) creeping stems, close to the ground and frequently buried under leaves and other forest débris, and (2) upright stems, very much branched in some species and bearing the cones like clubs at their ends. Some of the larger species are very common in the northern woods, the long, creeping stems often growing thickly over the ground. The stem is generally quite woody in structure, and the leaves are evergreen. They are much used in holiday decoration, and certain species are in danger of extinction, since the club mosses reproduce very slowly.

Fig. 286. A club moss (*Lycopodium annotinum*)

Modified after Kerner

321. The cone of Lycopodium. In some species of *Lycopodium*, as *L. Selago*, the spore leaves (sporophylls) have the same form and grouping as the vegetative leaves so that there is no cone distinct from the rest of the stem. But most of the forms have very clearly defined cones, which are sometimes raised on long stalks, as in *L. complanatum*. The sporophylls are generally scale-like and closely set (Fig. 287, *A*, *B*). Each spore leaf bears a single, large, sac-like sporangium (Fig. 287, *C*) at its base, which develops from a group of cells. The spores (Fig. 287, *D*) are formed in groups of four (tetrads) in the spore mother cells. They are very minute and are produced in such immense numbers that they are collected in quantity as the lycopodium powder of apothecary shops, used in dusting pills to keep them from sticking together as well as for other purposes. This powder is also employed in the manufacture of fireworks under the name of vegetable sulphur.

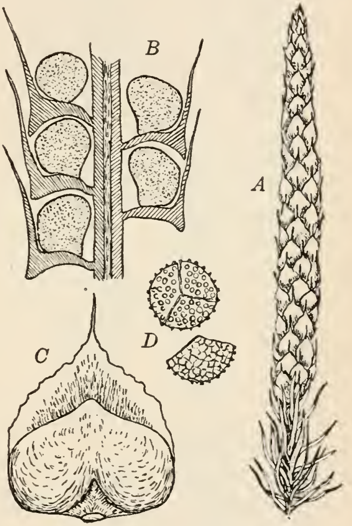

Fig. 287. The cone of a club moss (*Lycopodium annotinum*)

A, the cone, showing overlapping sporophylls; *B*, diagram of a longitudinal section, illustrating the form and position of the sporophylls and sporangia; *C*, the inner face of a sporophyll, showing the large sporangium; *D*, two views of spores from a group of four (tetrad)

322. The gametophytes of Lycopodium. The gametophytes of the club mosses in our northern woods must be uncommon, if they are developed at all, for they have never been found. It is probable that the sporophytes reproduce chiefly or perhaps entirely by vegetative branching of their stems and in some forms by curious buds. The gametophytes of some tropical lycopods are however known and have been studied. They are small, tuberous bodies (Fig. 288) generally subterranean and practically destitute of chlorophyll, like those of the moonwort and adder's-tongue. They are therefore saprophytic, and associated with them are fungal filaments to form a mycorrhizal relation (Sec. 278). The sexual organs are sunken structures. The sperms are two-ciliate.

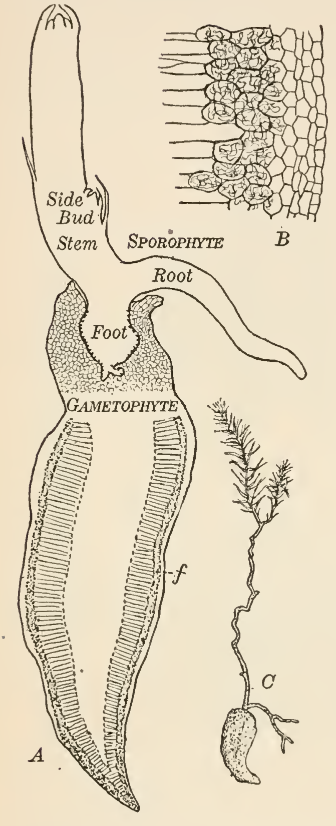

FIG. 288. Gametophytes and young sporophytes of a club moss (*Lycopodium complanatum*)

A, gametophyte with young sporophyte: *f*, tissue filled with the filaments of a fungus situated just outside a layer of palisade cells. *B*, the fungus-infected tissue. *C*, a young club moss still attached to the subterranean gametophyte. —*A*, *B*, from material of Bruchmann prepared by Miss Lyon; *C*, after Bruchmann

The embryo sporophyte remains attached to the gametophyte by a large foot (Fig. 288) for a long time after the stem and root are developed, and must obtain much nourishment from the gametophyte, as in the case of the ferns.

323. Selaginella. *Selaginella* is readily distinguished from *Lycopodium*. The leaves in most species are arranged in four rows, two rows of smaller leaves on the upper surface and two rows of larger leaves somewhat at the sides (Fig. 289, *A*). The cones also have four rows of spore leaves (sporophylls) and are consequently four-angled. The spores are of two sizes, and the type is perhaps the best illustration of heterospory in the pteridophytes. Forms of *Selaginella* are frequently called "little club mosses," for many of them are much more delicate than the lycopods. But some tropical species, frequently cultivated in greenhouses, are large, much-branched, and bushy plants, very graceful and decorative. Some forms grow in dry situations on sand and rocks, in Mexico and the Southwest. One species (*S. lepidophylla*) is frequently sold in the North under the name of "resurrection moss." This plant protects itself during drought by rolling up the branches to form a compact ball. When moistened the branches spread out and become fresh and green.[1]

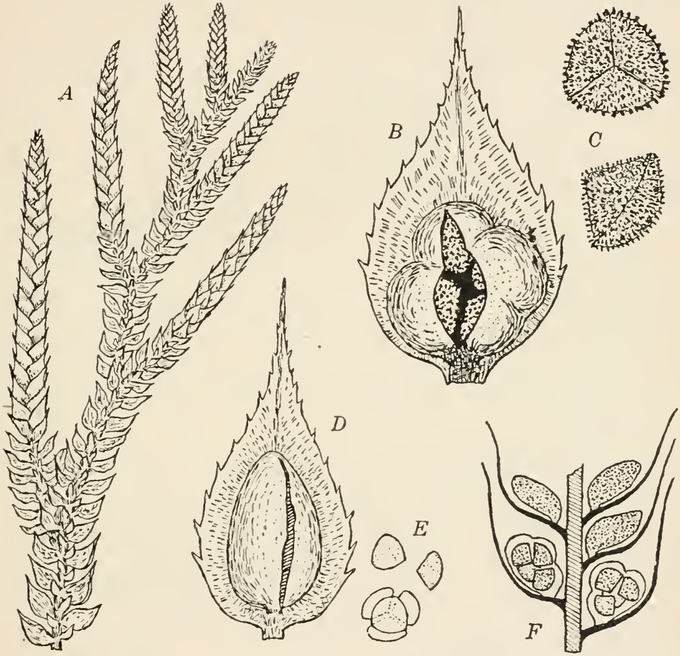

Fig. 289. *Selaginella Martensii*

A, branch bearing cones and showing the leaf arrangements; *B*, inner face of a megasporophyll, showing the large megasporangium containing a group of four megaspores (tetrad); *C*, two views of megaspores; *D*, inner face of microsporophyll, showing microsporangium; *E*, microspores; *F*, diagram of a longitudinal section of cone illustrating position of microsporophylls and megasporophylls and their microsporangia and megasporangia

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[1] A botanist states that the plants sold in the North will absorb moisture and unroll, but are generally "dead" beyond recovery.

324. The cones of Selaginella. The cones of *Selaginella* are not as large as those of *Lycopodium*, but they are much more complex in structure. The sporangia are of two sorts, both developing singly from a group of cells on the stem just above the origin of the spore leaves and later becoming attached to their bases. The sporangia near the lower part of the cone (Fig. 289, *B*) produce from one to eight very large megaspores, and frequently a group of four (tetrad). The sporangia higher up on the cones (Fig. 289, *D*) are smaller and develop a great number of minute microspores, also in tetrads. Selaginella has, then, different sporangia for the two forms of spores, microspores and megaspores, which are accordingly called *microsporangia* and *megasporangia*. Furthermore, these sporangia are borne upon different spore leaves, which are consequently termed *microsporophylls* and *megasporophylls*. It is important to note that the few megaspores which mature are nourished and grow at the expense of neighboring spore mother cells which become disorganized.

325. The gametophytes of Selaginella. The microspore develops a reduced and degenerate male gametophyte, as in *Marsilia* (Sec. 313). There is a small sterile cell (prothallial cell) and two groups of sperm cells in a very simple cellular structure probably representing an antheridium (Fig. 290, *A*). The sperms are two-ciliate (Fig. 290, *B*).

The megaspore develops a female gametophyte which is larger than that of *Marsilia*, but it is the same sort of a reduced structure, dependent upon food stored by the sporophyte within the megaspore. This gametophyte at maturity fills the megaspore, and bursting through the spore wall it presents an exposed surface upon which several sunken archegonia are developed (Fig. 290, *C*). The female gametophyte actually begins its development before the megaspore has attained its full size in the megasporangium. It is thus parasitic upon the sporophyte during its early history, a habit which is universal in the seed plants, but among the pteridophytes it is only found in *Selaginella*.

There are some other life habits of *Selaginella* wonderfully suggestive of the way in which seed and the seed habit arose. It is known in some species, as *S. rupestris*, that the microspores are thrown out from the sporangia on the upper part of the cone and sift down like pollen grains among the megaspores

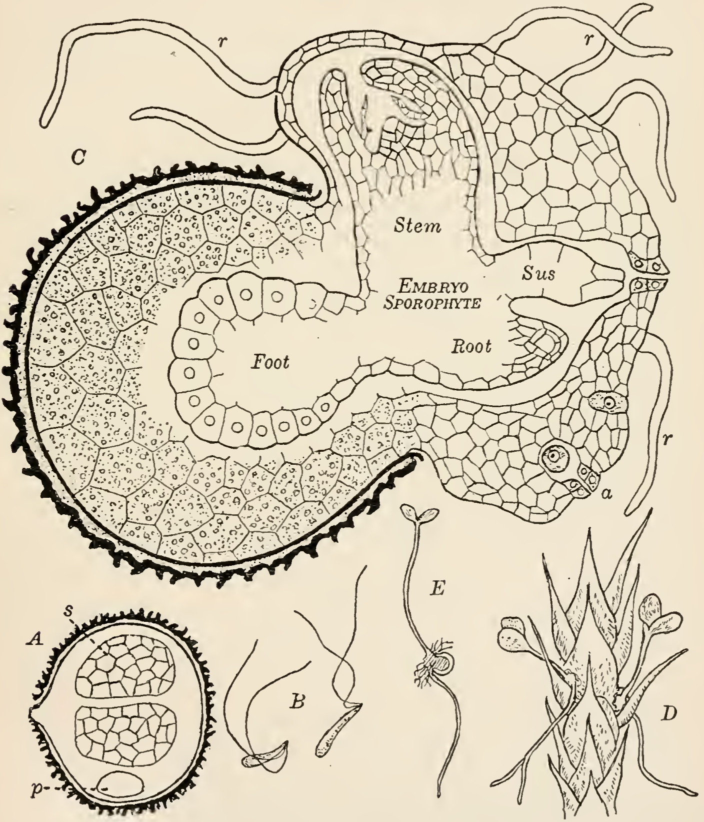

FIG. 290. The gametophytes and embryo of *Selaginella*

A, male gametophyte contained within the microspore: *p*, persistent nucleus of prothallial cell; *s*, two groups of sperm mother cells. *B*, two-ciliate sperms. *C*, female gametophyte containing an embryo sporophyte: *a*, archegonium; *r*, rhizoids. *D*, young sporophytes held by the spore leaves of the cone. *E*, a young sporophyte still attached to the megaspore. — *B*, after Belajeff; *A*, *C*, *D*, adapted after notes and sketches of Miss Lyon into the split megasporangia below. The sperms are formed and set free in the moisture of such situations, and the eggs of the gametophytes may be fertilized while the megaspores are still retained within the megasporangium. The young sporophytes as they develop are thus actually held by the sporophylls of the parent sporophyte (Fig. 290, *D*) until they reach a considerable size and fall off. These habits should be noted and this paragraph read again after the life history of the seed plant is thoroughly understood.

The development of the young sporophytes of *Selaginella* and also of *Lycopodium* has features resembling those of the seed plants. The early divisions of the egg establish a structure called the *suspensor* (Fig. 290, *C*, *Sus*), which carries the developing embryo down into the midst of the tissue of the gametophyte, where it can draw nourishment from all of the cells around it. A large foot is developed (Fig. 290) which absorbs food from that portion of the gametophyte which lies in the megaspore, so that the embryo sporophyte is actually nourished with food stored in the megaspore by the sporophyte of the previous generation.

326. Life history of Selaginella. *Selaginella* is an excellent type with which to illustrate the life history of a heterosporous pteridophyte. Since two forms of spores, microspores and megaspores, are present, there are two forms of gametophytes, male and female, and this feature complicates the relatively simple life-history formulæ of bryophytes and homosporous pteridophytes (Secs. 285, 310).

The life history of *Selaginella* is as follows:

$$\textit{Sporophyte} < \begin{matrix} \textit{microspore} - \textit{Male Gametophyte} - \textit{sperm} \\ \textit{megaspore} - \textit{Female Gametophyte} - \textit{egg} \end{matrix} > - \textit{Sporophyte}, \text{ etc.}$$

This in abbreviated form becomes

$$S < \begin{matrix} mi\ sp - M\ G - s \\ me\ sp - Fe\ G - e \end{matrix} > - S, \text{ etc.,}$$

which when carefully studied is essentially the same as the general life-history formula of bryophytes and pteridophytes (Secs. 285, 310), namely,

$$G <_{e}^{s}> - S - sp - G <_{e}^{s}> - S - sp - G, \text{ etc.}$$

The differences lie in the fact, above mentioned, that there are two forms of spores, microspores and megaspores, which develop, respectively, male and female gametophytes, a complication which was introduced with heterospory and which is present, as will appear later, in the life histories of seed plants (Sec. 356).

327. Summary of Selaginella. *Selaginella* is the highest of the pteridophytes and the most important because of the evolutionary principles which it illustrates, leading up to the seed habit. The first three of these principles are also illustrated by *Marsilia* and *Isoetes,* but the fourth and fifth are new. They are (1) the establishment of heterospory resulting in the separation of male and female gametophytes; (2) the reduction or degeneration of the gametophyte, which becomes dependent upon food stored in the microspores and megaspores; (3) provision in the megaspore for the nourishment of the embryo of the succeeding sporophyte generation; (4) the early parasitic relation of the female gametophyte within the megasporangium upon the sporophyte; (5) the occasional habit of developing the young sporophyte while the megaspore is still retained within its parent megasporangium.

328. Isoetes. The species of *Isoetes* are known as quillworts. Their position among the pteridophytes is a matter of dispute, and some botanists place them with the ferns (*Filicineæ*), but the anatomy of the sporophytes is more like that of the club mosses than any other group. They have a peculiar rush-like habit of growth, the long leaves arising in clusters around a short stem (Fig. 291, *A*). Some forms are aquatic, growing on mud at the bottom of ponds, while others are usually found out of water.

Isoetes is heterosporous, and the spores are developed in sunken sporangia at the bases of spore leaves (Fig. 291, *B*, *s*). The spore leaves are differentiated so that only the outermost develop megaspores and are consequently megasporophylls, while the innermost are microsporophylls, producing only microspores. Male and female gametophytes are developed slowly in the microspores and megaspores, respectively, and are reduced or degenerate sexual plants (Fig. 292, *A*, *C*), almost as simple as

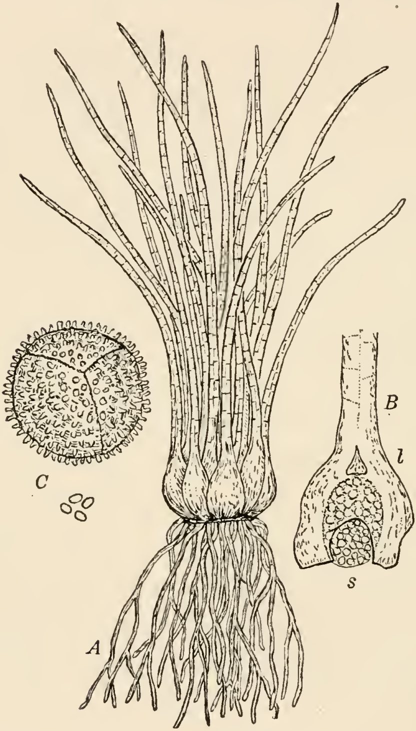

FIG. 291. The quillwort (*Isoetes echinospora*)

A, habit sketch. *B*, base of megasporophyll, showing inner surface: *s*, sporangium, containing the large megaspores; *l*, ligule. *C*, a group of microspores below, and a large megaspore above, showing comparative size those of *Marsilia*. Having no chlorophyll, they depend upon food stored in the megaspore, as in *Marsilia* and *Selaginella*. The young sporophyte also makes use of food in the megaspore as in these other two heterosporous pteridophytes above mentioned. The sperms (Fig. 292, *B*) are somewhat coiled and many-ciliate, resembling in this respect those of the *Filicineæ*. The life-history formula is the same as that of Selaginella (Sec. 326).

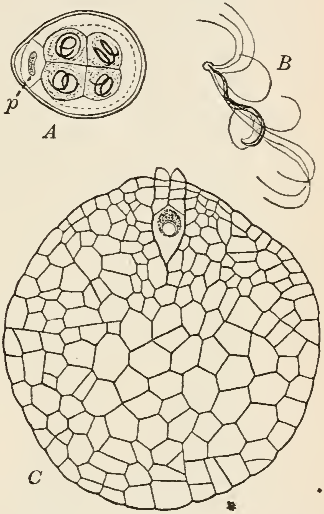

Fig. 292. Gametophytes of the quillwort (*Isoetes*)

A, male gametophyte within the microspore: *p*, prothallial cell; four sperm mother cells shown within the reduced antheridium. *B*, sperm. *C*, section of female gametophyte removed from megaspore, showing sunken archegonium. *A*, *C*, *Isoetes echinospora*. — *A*, *C*, after Campbell; *B*, after Belajeff

FOSSIL PLANTS AND COAL

329. Fossil plants. Plant remains are not generally preserved as fossils, partly because they do not often have hard parts, such as the shells and bones of animals, and partly because the larger forms grow on land where they are subject to rapid decay. So the record of plant life in former geological ages is poor as compared with that of animal life. However, there are some very wonderful deposits of plant remains forming the hard and soft coal beds, which deserve brief mention here, since most of the plants composing them are fossil pteridophytes.

During the Devonian and Carboniferous Ages the most conspicuous vegetation was represented by tree ferns and relatives of the horsetails and club mosses, together with certain very primitive gymnosperms. These plants reached the height of trees and formed forests on the land and in the marshes (see Plate VIII). The *Calamites* (Plate VIII, 2) were gigantic horsetails, so nearly like the living forms of *Equisetum* that we can readily picture their appearance along the margins of swamps and streams. Curiously some of the *Calamites* were heterosporous, although all of the living types of the *Equisetineæ* are homosporous. The ancient representatives of the club mosses (Plate VIII, 3, 4) were among the largest plants of those times, reaching the height of one hundred feet or more. Some of them were true lycopods, and others, as *Lepidodendron* and *Sigillaria*, were evidently close relatives of the club mosses. Their large trunks were covered with leaves, which fell off, leaving curious, diamond-shaped scars that are very conspicuous on the fossil stems. The earliest seed plants arose in these ages, but they were far outnumbered by the pteridophytes. They were gymnosperms of the group *Cordaiteæ* (Plate VIII, 5), but with very little resemblance to any living forms. The fructifications of some of these primitive forms, somewhat intermediate between spermatophytes and pteridophytes, are occasionally so well preserved that we can learn something of the structure of the gametophytes developed by the spores. It is possible that we shall later know much more about the origin of the seed plants and the seed habit from the study of these fossils.

After the Carboniferous Age the tree ferns, horsetails, and club mosses became less abundant, and gymnosperms, like the cycads and conifers, increased in numbers and became the dominant forest types. There was an age of cycads in a later period (Jurassic), when the earth was covered with these plants as far north as Greenland and the climate must have been tropical from pole to pole. We know very little about the earliest forms of angiosperms. They do not appear abundantly as fossils until a later period (Cretaceous), after the age of cycads (Jurassic), although they doubtless had their origin much earlier, for many insects were present which must have had the habit of feeding on pollen or nectar.

It is clear that the horsetails and club mosses of the present time are merely the remnants of this ancient flora once dominant

Plate VIII. A probable landscape in the Carboniferous Age

1, a tree fern ; 2, *Calamites*, giant relatives of the horsetails ; 3, 4, *Lepidodendron* and *Sigillaria*, giant club mosses; 5, *Corduites*, a primitive gymnosperm. — After Potonié

and perhaps as luxuriant as the tropical forests of to-day. They have survived by adjusting themselves to very different life conditions from those of Carboniferous times, and by adopting life habits which remove them as far as possible from competition with the prevailing vegetation forms of to-day (trees, grasses, herbs, etc.). The degenerate, saprophytic gametophytes of *Lycopodium* illustrate well how far such changes of life habits may extend.

330. Coal. Coal was formed during a number of periods in the earth's history, but the most extensive deposits were laid down during the Carboniferous Age (frequently called the coal age), forming the so-called coal measures. The luxuriant pteridophyte vegetation of tree ferns, horsetails, and club mosses formed deposits in swamps over immense areas, probably in much the same way as peat is being formed to-day. Such plant deposits from time to time became covered with sediment by the sinking of the land. And since the land alternately rose and sank, successive layers or beds of plant remains were laid down. These remains became finally buried under heavy deposits of sediment, which pressed them into compact beds of the carbonaceous matter called *coal*.

Coal is of two sorts: (1) soft or bituminous coal, which is hardly more than half pure carbon, the rest being composed of a variety of carbon compounds, and (2) hard or anthracite coal, which may be 90 per cent pure carbon. Hard coal represents a greater degree of change than soft coal, the oils and other products having been driven off under pressure by the heat of the earth. The coal beds vary in thickness from small layers of only a few inches to deposits a hundred feet deep. Those of the United States cover several hundred thousand square miles, of which perhaps fifty thousand square miles are being worked. Vast as are these coal beds in the United States, there are deposits in other lands, as in China, of even greater extent. The coal supply of China is estimated as enough to last the world seven hundred years. The total deposits of pteridophyte vegetation were very much thicker than the coal beds which they formed, for it has been estimated that it took about five feet of plant remains to make one foot of coal.

It is interesting to think of the part which the pteridophyte flora of the Carboniferous Age plays in the present life and economic activities of the world, giving us a fuel whose carbon was taken ages ago from the air, which was then much more heavily charged with carbon dioxide than is the atmosphere of to-day.

THE ORIGIN AND EVOLUTION OF THE PTERIDOPHYTES

331. The origin of the pteridophytes. The pteridophytes undoubtedly arose from a bryophyte ancestry, when the sporophyte generation, in some forms having a structure capable of doing chlorophyll work, developed a root system and vascular tissues, and taking the land habit *became independent of the gametophyte.* This was one of the most important forward steps in the evolution of the higher plants, for it gave the sporophyte complete freedom to live and grow to its maximum size. It marked a turning point in plant evolution, for after that the sporophyte became the most complex and conspicuous phase of the life history, and the gametophyte grew less prominent, until finally in the seed plants the sexual generation becomes actually dependent or parasitic upon the asexual generation, a relationship which is exactly the reverse of that between the gametophyte and sporophyte in the liverworts and mosses. These very important results in the evolution of plants are summarized in Chapter XXIX, The Evolution of the Sporophyte and Degeneration of the Gametophyte.

There are no bryophytes that show clearly how the root system arose, but we can easily understand that so complex a sporophyte as that of *Anthoceros* (which has chlorophyll-bearing tissues with stomata, and a long, indefinite period of growth) would at once become an independent plant, if it could develop a root system. For this reason, *Anthoceros* (Sec. 290) is generally considered the form among the bryophytes most closely approaching the pteridophytes in its structure and possibilities of development.

332. The evolution of the pteridophytes. After the sporophyte became independent of the gametophyte, the next important advance was the development of the lateral spore-bearing and vegetative organs called *fronds.* Then came the differentiation of the fronds into vegetative leaves, given up entirely to chlorophyll work (photosynthesis), and spore leaves, or sporophylls, devoted chiefly or wholly to spore production. *With this also came the massing of the sporophylls in cones, which was really the beginning of the structures called flowers in the seed plants.*

Finally, the condition of heterospory was attained independently in several groups of the pteridophytes, as the water ferns, *Selaginella,* and *Isoetes.* Heterospory soon led to very significant changes in the structure and behavior of the gametophyte generations. They became differentiated in sex, the microspores producing male prothalli, and the megaspores female ones. Furthermore, the gametophytes became greatly reduced, finally depending wholly, or almost wholly, on food stored in the spores. The food in the female gametophyte also came to contribute to the development of the embryo sporophyte, which was thus furnished with food by the sporophyte of the previous generation. At last, in the highest form, *Selaginella,* the female gametophyte, begins its development while still retained within the megaspore, a condition approximating very closely to the seed habit.

SUMMARY OF THE PTERIDOPHYTES AND THEIR ADVANCES OVER THE BRYOPHYTES

333. Summary of the pteridophytes. The chief characters of the pteridophytes and their advances over the bryophytes are:

1. The development of a leafy shoot and root system with vascular tissues in the sporophyte generation, rendering it

independent of the gametophyte, giving it the land habit, allowing it to attain a large size, and making it by far the most conspicuous phase in the life history.

2. The development and differentiation of fronds into vegetative leaves and sporophylls, and the grouping of the latter into cones.

3. The development of heterospory, which differentiated the gametophytes as male and female in sex.

4. The degeneration of the gametophytes (in heterosporous forms) so that they finally became dependent upon food supplied by the sporophyte in the spore. In *Selaginella* the female gametophyte even begins its development at the expense of neighboring cells in the megasporangium. These conditions are an exact reversal of the relations between the generations which exist in the bryophytes.

The three classes of the *Pteridophyta* are readily distinguished by the following characters:

Class I. Filicineæ. Fronds large and few in number; those bearing spores generally similar to the strictly vegetative leaves and not grouped in cones.

Class II. Equisetineæ. Leaves reduced to mere scales, forming sheaths around jointed stems, which have many peculiarities of structure; sporophylls of peculiar form, each bearing several sporangia, and grouped in a characteristic cone.

Class III. Lycopodineæ. Vegetative leaves, small and very numerous (except in *Isoetes*), covering the stem; sporophylls generally grouped in cones, each bearing a single sporangium; gametophytes much degenerate, especially in the heterosporous *Selaginella* and *Isoetes;* sperms two-ciliate, except in *Isoetes,* and not spiral, and many-ciliate as in the *Filicineæ* and *Equisetineæ.*

CHAPTER XXVI

ALTERNATION OF GENERATIONS

334. The protoplasmic basis of an alternation of generations.* The history of the alternation of generations in plants has now been traced from the relatively simple beginnings in the thallophytes, as illustrated by the life histories of the red algæ (Sec. 246) and sac fungi (Sec. 266) through the more clearly defined conditions in the liverworts and mosses, and also through the ferns, horsetails, and club mosses. It is clear that in the latter groups and the pteridophytes the asexual, or sporophyte, generation had become much the more complex of the two, and that the sexual generation, or gametophyte, had begun to degenerate. This degeneration is carried much further in the seed plants, as will be described in Chapter XXVIII, and summarized in Chapter XXIX.

It is now time to try to determine some of the reasons for the establishment of a sporophyte generation following the gametophyte one, or the basis in the protoplasm itself of the alternation of sexual and asexual generations. The basis undoubtedly rests on the effects of the sexual process upon the nature of the protoplasm in the succeeding generation. The union of gametes is so great a physiological stimulus that the sexually formed cell (generally a fertilized egg) is given the possibilities of a development different from that of either parent plant or gametophyte; for the protoplasm of a fertilized egg is not the same as that of either gamete which entered into its formation. It is a mixture of protoplasms and therefore must be different from the protoplasm of the parent plants, and this difference is the basis for

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* To the Instructor: In a brief course or with immature students this chapter should be omitted.

the peculiarities of the generation which arises from a sexually formed cell.

Protoplasm has so far proved much too complex for an analysis into the structures which determine its qualities and possibilities of development; that is, we do not know why the egg of a fern develops into a fern and that of a club moss into a club moss; both are cells with a general similarity of cell structure. But the possibilities of fern and club moss are nevertheless present in the respective eggs, and the one could not possibly be made to produce the other plant. It is generally believed that the characteristics of eggs are determined by the structure of their protoplasm, represented perhaps by means of the invisible molecules and groups of molecules in its chemical and physical composition. The structures that are assumed to give distinct character or possibilities of development to protoplasm are called *rudiments.*

It is doubtful whether we shall ever be able to distinguish the rudiments, but there are some larger structures in the cell which with care can be followed through the cell divisions from generation to generation. The most interesting of these are the *chromosomes,* which are very characteristic structures most clearly seen during the processes of nuclear division (Sec. 199). The substance of the chromosomes, called *chromatin,* is the most important material in the nucleus. Chromatin can be deeply colored or stained in thin sections of tissue after special methods of treatment. It is present in the resting nucleus, generally in the form of an irregular network. The chromosomes are formed from the chromatin and appear during the early stages of nuclear division. Each chromosome then divides into halves, and the two sets of daughter chromosomes are distributed with each nuclear division.

It is an important fact that the number of chromosomes for the nuclei of each plant is fixed, and the number is usually not very large. Thus the gametophytes of a red alga (*Polysiphonia,* Sec. 245) have about 20 chromosomes, but those of the liverwort (*Anthoceros*, Sec. 290) have only 4 and the fern (*Osmunda*) 12. The most important feature of the process of fertilization is the union of the two gamete nuclei, that of the sperm with that of the egg. These nuclei have an equal number of chromosomes in the same species (the number characteristic of the gametophyte), and the egg and sperm are therefore equivalent in their nuclear structure, whatever may be the differences in their size. This nuclear fusion doubles the number of chromosomes, and the fertilized egg begins the development of the sporophyte (when present) with twice as many chromosomes as the gametophytes which produced the eggs and sperms.

The double number of chromosomes appears in all of the nuclear divisions throughout the development of the sporophyte up to the time of spore formation. Thus the sporophyte phases of *Polysiphonia* have about 40 chromosomes, the sporophyte of *Anthoceros* 8, and *Osmunda* 24. The lilies have 24 chromosomes, and the gametophyte phase only 12. The chromosomes have been counted in more than fifty different kinds of plants, mostly seed plants, and it is established that sporophytes have normally double the number of chromosomes of their respective gametophytes.

Spore formation at the end of the sporophyte generation is a very significant period in the life history, for at this time the double number of chromosomes is reduced by half. The spores have then the original number of the gametophyte. The reduction of the chromosomes is effected by processes too complicated to be described here, but the formation of the asexual spores in groups of four, called *tetrads* (see Figs. 204, 245, 258, 289, 298, 302, 304), is rather characteristic of the phenomenon. There are thus fundamental reasons for the identical methods of spore formation in the bryophytes and pteridophytes, and, as will appear later, for the methods of pollen formation and the embryo sac in the seed plants. For the same reasons, groups of four spores, (tetraspores), are developed at the end of the sporophyte generation in the red algæ.

The chromosomes are generally believed to be the actual bearers of the qualities (represented perhaps by rudiments) which are *inherited,* that is, passed on from one generation to the next. The chief reasons for this view are their importance as the essential structures of the nucleus, their regular behavior throughout the cell divisions, and the evidence that they never lose their identity completely, even in the resting nucleus, but remain perhaps as the only permanent organs in the cell.

335. The life-history formula, showing the chromosome count. The life-history formula which has been employed for the bryophytes and pteridophytes becomes much more interesting when considered in reference to the chromosome count. The formula has been:

$$\mathit{Gametophyte} < \begin{matrix}\mathit{sperm}\\ \mathit{egg}\end{matrix} > - \mathit{Sporophyte} - \mathit{asexual\ spore}$$

$$- \mathit{Gametophyte},\ \text{etc.}$$

Representing the gametophyte number of chromosomes by x and the sporophyte number by $2x$, these may accompany the formula as follows:

$$\underset{x\ \mathit{chromosomes}}{\mathit{Gametophyte}} < \begin{matrix}\mathit{sperm}\\ x\ \mathit{chro.}\\ \mathit{egg}\\ x\ \mathit{chro.}\end{matrix} > - \underset{2x\ \mathit{chromosomes}}{\mathit{Sporophyte}} - \underset{x\ \mathit{chromosomes}}{\mathit{asexual\ spore}}$$

$$- \underset{x\ \mathit{chromosomes}}{\mathit{Gametophyte}},\ \text{etc.}$$

Examining this formula, it is clear that there are two periods when the number of chromosomes changes abruptly: (1) at fertilization, when the number is doubled, and (2) at spore formation, when the number is reduced. The fertilized egg develops into the sporophyte because its protoplasm has different qualities from that of the gametophyte. The asexual spore develops into the gametophyte because its qualities have become again the same as those of the former gametophyte generation. Spore formation, then, in bryophytes and pteridophytes is a return of the plant in its life history to the conditions of ancestral gametophytes.

336. The origin of the sporophyte. It seems clear that the sporophyte had its origin through the stimulus of the union of gametes, and especially the union of gamete nuclei, to give a fusion nucleus with double the number of chromosomes characteristic of the gametophytes. It is probable that there is a reduction of this number in many thallophytes before or during the germination of the zygospore or oöspore, so that there is no opportunity for a sporophyte generation. This condition has been reported for *Coleochæte* (Sec. 222), and it is probably also true of *Œdogonium*, *Spirogyra*, the desmids, *Vaucheria*, *Ulothrix*, and other types.

The sporophyte arose when nuclear divisions appeared with the double number of chromosomes, thus postponing the time of chromosome reduction to a later period in the life history, which became generally characterized by the formation of asexual spores in tetrads. Sporophytes undoubtedly appeared thus in several groups of plants entirely independently of one another, as illustrated in the divergent lines of development of the red algæ, the sac fungi, the *Dictyotaceæ* (a small group of the brown algæ), and the bryophytes leading up to the pteridophytes and spermatophytes.

337. Summary. The alternation of generations in plants takes on added interest when considered in relation to the behavior of the chromosomes, for the importance of the two critical stages in the life history — (1) fertilization, and (2) spore formation — becomes at once apparent. Fertilization doubles the number of chromosomes in the egg and gives it the possibilities of the sporophyte's development. Spore formation reduces the double number of chromosomes by half and brings the plant's protoplasm back to the condition where it may develop the gametophyte. The two processes follow one another as the life history is repeated again and again with machine-like regularity, and there is undoubtedly a chemical and physical basis for the life history. And, as before stated, it is generally believed that the chromosomes hold the rudiments that determine in a broad way the programme of development, the double number defining the sporophyte generation.

It must not be supposed, however, that the life history unfolds entirely through the operation of forces *within* the organism, as a watch runs on the strength of the wound-up mainspring. While the organism is truly a machine, it is a machine which is constantly influenced by forces from without which modify its complex adjustments, and, above all, it is a self-perpetuating machine which makes its own repairs.

There are two prominent theories respecting the manner in which an organism develops from an egg or other reproductive cell. The first, called *preformation*, assumes that the characters of the adult are preformed or represented in miniature by rudiments or other structures in the protoplasm. Development is, therefore, something like the unfolding of a bud, and the results are determined by conditions within the organism. The second theory, termed *epigenesis*, is not willing to grant such a complicated architecture to protoplasm, but holds that development is guided chiefly by conditions without the organism. It is probable that the correct interpretation lies between the two extreme views, that the cell does have a complicated structure far beyond our present possibilities of knowledge, but that the processes of development are largely guided and controlled by outer influences.

CHAPTER XXVII

HETEROSPORY

338. Heterospory.* Heterospory arose in the pteridophytes with the establishment of two sizes of spores, called *megaspores* (large spores) and *microspores* (small spores). Heterospory and the independence of the sporophyte are the chief contributions of the pteridophytes to the progress of plant evolution. The establishment of megaspores and microspores was merely the beginning of a number of far-reaching developments in plants, all of which are really parts of the general principle of heterospory. They all reach their highest degrees of specialization in the seed plants, as will be described in the next chapter and summarized in Chapter XXIX, but most of them are clearly illustrated in the pteridophytes.

These developments resulting from heterospory are:

1. The gametophytes became differentiated in sex so that the megaspore always develops a female gametophyte and the microspore a male gametophyte.

2. The sporangia assumed two forms: *megasporangia* devoted to the production of megaspores and *microsporangia* devoted to the production of microspores, as illustrated by *Marsilia, Isoetes, Selaginella,* and, as will appear in the next chapter, the seed plants.

3. The spore leaves, or sporophylls, were differentiated into *megasporophylls* and *microsporophylls* which develop, respectively, megasporangia and microsporangia, as illustrated by *Isoetes, Selaginella,* and the seed plants; the sporophylls of *Marsilia* bear both forms of sporangia.

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* To the Instructor: In a brief course or with immature students this chapter should be omitted.

4. A tendency was developed to reduce the number of megaspores by sacrificing many of the cells which might be fertile so that relatively few megaspores are formed, but these are very large and richly supplied with food material, as illustrated by *Selaginella* and the seed plants. This principle is clearly similar to that by which plants have found it advantageous to produce a limited number of large eggs well stocked with food, even at the sacrifice of cells which may have been originally gametes, such as the canal cells in the archegonium.

5. The gametophytes degenerated, as self-supporting green plants, to a condition in which they lost their chlorophyll and became dependent upon food stored in the megaspores and microspores and even live somewhat parasitically upon the sporophytes, as is illustrated in the early stages in the development of the female gametophyte of *Selaginella* and in the gametophytes (pollen tube and embryo sac) of the seed plants.

There is another important advance in plant evolution which is closely related to heterospory, but may be treated to better advantage in the account of the origin of the seed habit (Sec. 367). This advance arose in the seed plants when the megaspore became retained within the megasporangium (a portion of the ovule), so that the female gametophyte (embryo sac) developed like a parasite upon the parent sporophyte, and the male gametophyte (pollen tube) was required to grow down to the female gametophyte somewhat parasitically through the tissues of the ovule to bring about the fertilization of the egg cell.

339. Sexual characteristics given to the megaspore and microspore by means of heterospory. The megaspore and microspore are of course asexual spores because they are formed by an asexual plant, the sporophyte. They are simply specialized forms of the similar spores present in the liverworts, mosses, the common ferns, horsetails, and lycopods, as shown by their similar origin in tetrads at the end of the sporophyte generation.

But when the microspore and megaspore became clearly differentiated through heterospory from the earlier conditions of homospory they took on certain characteristics of sex. *This does not mean that the microspores and megaspores became gametes, for their spore nuclei have never become sexual nuclei in any group of plants.* But microspore and megaspore did assume sexual characters to this extent that they always give rise, respectively, to male and female gametophytes.

Furthermore, the degeneration of the gametophytes steadily reduced the number of the nuclear divisions between the germination of these spores and the formation of the gametes until the gamete nuclei have been brought very close indeed to the spore nuclei. An examination of the figures of the male gametophytes of *Marsilia* (Fig. 282, *A*), *Selaginella* (Fig. 290, *A*), and *Isoetes* (Fig. 292, *A*) will show that there can hardly be more than from six to ten nuclear divisions in these types before the sperms are developed. There are even fewer nuclear divisions in some groups of seed plants where the degeneration of the gametophyte is carried much further than in the pteridophytes. Some forms of angiosperms present but a single division of the spore nucleus before the female gamete nuclei are formed, as in the embryo sac of the lily (Sec. 360, note), and there are only two nuclear divisions in the male gametophytes (pollen grain and tube) of the angiosperms.

This gradual transference of sexual characteristics to portions of the asexual generation, accompanying the reduction of the sexual generation, is one of the most interesting results of the evolution of the sporophyte and degeneration of the gametophyte (summarized in Chapter XXIX), for it makes clear many puzzling conditions in the seed plants. Thus it shows why the pollen grain (which is a microspore) is really *functionally* a male reproductive structure and the stamen a male organ; and why the carpels and pistil are *functionally* female organs, even though they have had their origin on asexual plants (sporophytes).

CHAPTER XXVIII

THE SPERMATOPHYTES AND THE SEED HABIT

340. The spermatophytes.* The division *Spermatophyta* (meaning seed plants) contains not only the groups frequently called "flowering plants" but also other groups which do not have flowers in the popular sense of the word, for the reproductive organs are borne in cones or clusters which are not at all showy, but rather inconspicuous. These are, however, flowers in the scientific sense, as are also the cones of the horsetails and club mosses. The spermatophytes have also been called *phanerogams*, or *phænogams* (meaning evident marriage), to distinguish them from all the lower groups of plants which were called *cryptogams* (meaning hidden marriage). However, this separation was made before the sexual processes of the lower plants were understood, for as a matter of fact they are much more evident than the complicated ones in the seed plants. The seed is a more significant structure in the group than the flower, so the name *spermatophytes* has in recent years come into general favor.

The seed plant, like the fern, is a sporophyte. There is a gametophyte generation in the life history which is, however, so much reduced in structure that it can only be understood by a careful study of the reproductive processes in seed formation. It is the main purpose of this chapter to make clear the position of the gametophyte generation in the life history, together with the origin and evolution of the flower. The structure and physiology of the sporophyte are considered in Part I,

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* TO THE INSTRUCTOR: The introduction to this chapter assumes that the life history of some seed plant, as the pine or lily, has been studied in the laboratory.

and only brief reference will be made to these features, which are treated there in detail and should follow this account if they have not already been studied.

341. The seed. The importance of the seed in the development of plant and also of animal life can hardly be exaggerated. For the plant it furnishes one of the surest means of reproduction not only because of protective structures, means of dispersal, long vitality, etc. (see Chapter XXXIII), but also because the embryo plant is carried so far forward in its development that it is able to take root and establish itself at once. And further to aid the embryo, the seed is a storage organ of the most condensed forms of food material found in plants. In this respect, also, the seed has proved a most important influence in shaping the habits and in a large measure the evolution of some forms of animal life; for the highest groups of animals live to a very great extent directly or indirectly upon food stored in seeds and certain fruits, finding there some of the richest and most nutritious proteid and carbohydrate foods. The animal life of the Carboniferous Age (coal age) and the periods immediately following comprised animals of great bulk of body, but of low nervous organization. They browsed on the vegetation like the hay and grass-eating animals (herbivora) of to-day, and like them their bodily structure and nervous system were adapted to such life habits. But, later, groups arose with digestive organs adapted to richer foods, and this diet became associated with varied life habits, which led to much higher types of nervous organization and bodily structure.

342. The morphology of the seed. The morphology of the seed can only be understood when the spermatophytes are studied in relation to the pteridophytes. The seed plant is a *heterosporous* sporophyte. The pollen grain is a microspore. The megaspores of the seed plant are never shed. They are retained in the megasporangium and never even lie freely as independent cells, but are always in close physiological relation to the tissue of the megasporangium. The cell which is the equivalent of the megaspore, or megaspore mother cell, is called the *embryo sac.* The megasporangium, termed the *nucellus,* with the embryo sac is contained within one or two protective envelopes, called *integuments,* and this group of structures constitutes the *ovule.* There is developed within the embryo sac a much-reduced female gametophyte which lives entirely on foods supplied by the sporophyte. The ovule at maturity then consists of the embryo sac (megaspore or megaspore mother cell) with the female gametophyte, the nucellus (megasporangium), and the integuments.

The female gametophytes are quite different in the two great subdivisions of seed plants (gymnosperms and angiosperms). In the first group (gymnosperms) several archegonia are generally formed, each containing a single large egg. In the second group (angiosperms) the female gametophyte is very much reduced and only one egg is formed. The fertilization of an egg leads at once to the development of an embryo sporophyte within the embryo sac. The embryo sporophyte of the second generation is thus nourished through the ovule by the parent sporophyte of the first.

The seed is a ripened ovule, that is, an ovule containing an embryo sporophyte so far along in its development that the seed may safely be separated from the parent plant. Morphologically, the seed is composed of tissues representing three generations: (1) the integuments and nucellus are of the parent sporophyte; (2) the embryo sac contains more or less tissue of gametophyte origin called *endosperm*[1]; (3) an embryo sporophyte of the next generation lies within the embryo sac.

343. Pollination and fertilization. The retention of the megaspore (embryo sac) within the megasporangium (nucellus) so that the female gametophyte is contained in the tissues of the sporophyte has resulted in modifications of the structure and

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[1] The endosperm of the angiosperm seed has special peculiarities involved with the fertilization of the egg and development of the embryo, as explained in Secs. 362 and 363.

life habits of the male gametophyte quite as remarkable as those of the female. These peculiarities are concerned with two distinct processes necessary to insure the development of seeds, namely, *pollination* and *fertilization.*

The pollen grain is a microspore developed in groups of four (tetrads) in pollen mother cells in essentially the same manner as the spores are developed in all bryophytes and pteridophytes (Fig. 302, *B*). The pollen grain forms a very much reduced male gametophyte, which is represented by the protoplasmic contents of the pollen grain and pollen tube. It would be useless for the male gametophyte to form and discharge sperms which could not possibly reach the embryo sac imbedded in the nucellus of the ovule. So the sperm-forming habits of the pteridophytes, bryophytes, and the algæ are generally given up, although curiously they still persist, as will be described later, in the cycads and *Ginkgo* (Sec. 348). The sperms are represented by two sperm nuclei developed by each male gametophyte and discharged from the tip of the pollen tube.

The pollen tube is an outgrowth from the pollen grain. Its purpose is to carry the sperm nuclei to the embryo sac, where one of the two may unite with the egg nucleus and fertilize the egg. In one of the two subdivisions of seed plants called the *gymnosperms* (meaning naked seeds) the pollen grains are applied directly to the ovules, and the pollen tube need only grow through the tissue of the nucellus (megasporangium) to reach the embryo sac. In the other large group called the *angiosperms* (meaning seeds inclosed in a vessel) the pollen tubes must penetrate a case (the pistil) which contains the ovules before they can reach the ovules themselves. There is a special receptive surface, called the *stigma,* upon this structure, where the pollen grains find moisture and other conditions favorable for their germination.

Pollination is the application of the pollen to the ovule or to the stigma. This application is effected in various ways, sometimes by the wind, sometimes by other chance processes, but many plants have developed elaborate devices to insure pollination, as through the visits of insects to flowers (see Chapter XXXII).

Fertilization is effected when the pollen tube pierces the embryo sac and one of its two sperm nuclei fuses with the egg nucleus.

When one considers the extraordinary modifications of the male gametophytes of the seed plants, the process of pollination and the development of the pollen tube seem quite as remarkable as the retention of the female gametophyte in the megasporangium. They are both essential features of the seed habit.

344. The flower. The term *flower* in the popular sense generally means some showy structure such as is only found in certain groups of the angiosperms. The flower in the scientific sense consists of a group of spore leaves, or sporophylls, with or without surrounding envelopes, which may or may not be showy. It has been defined as "a shoot beset with sporophylls." Since the seed plants are heterosporous, the spore leaves are either microsporophylls, called *stamens* (producing *pollen*), or they are megasporophylls, called *carpels* (producing *embryo sacs* in the ovules). The stamens and carpels of the gymnosperms are generally grouped in cones which resemble the cones of the horsetails and club mosses. But the carpels of the angiosperms form, often with adjacent tissue, closed cases called *pistils.*

It should be noted that the cones of the horsetails and club mosses are as truly flowers in the scientific sense as the cones of the gymnosperms, and also that certain groups of angiosperms (grasses, sedges, and most trees) have flowers which are not showy.

The material of this chapter will be treated under the following headings:

Subdivision I. The gymnosperms, or *Gymnospermæ.*
Subdivision II. The angiosperms, or *Angiospermæ.*
The origin of seed plants and the seed habit.
The evolution of the flower.
The classification of the angiosperms.
Summary of the spermatophytes and their relationships to the pteridophytes.

SUBDIVISION I. THE GYMNOSPERMS, OR *GYMNOSPERMÆ*

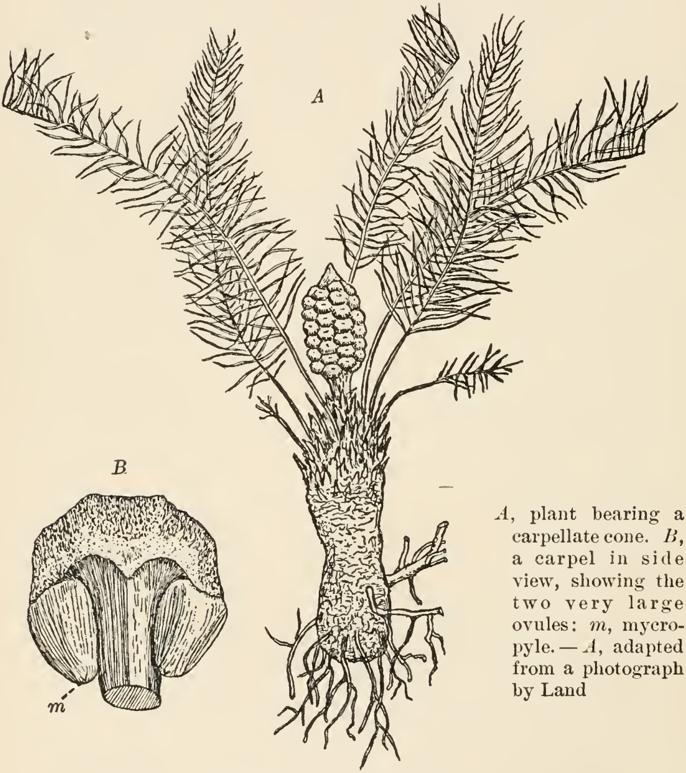
345. The gymnosperms. The gymnosperms (meaning naked seeds) are distinguished from the angiosperms because their seeds are borne exposed on the carpels. They comprise not only the familiar cone-bearing trees, or conifers, generally with needle-shaped leaves, such as the pines, spruces, firs, hemlocks, larches, cedars, etc., but also the large-leaved cycads, the straggling, shrubby *Ephedras*, the climbing *Gnetums*, and that interesting Japanese tree *Ginkgo*. The gymnosperms contain the most ancient groups of living seed plants, and the fossil remains of primitive types are found in the Carboniferous Age and even earlier periods, with those of the giant horsetails and club mosses (see *Cordaites*, Plate VIII). The study of ancient gymnosperms, together with a fossil group, *Pteridospermæ*, intermediate between the pteridophytes and spermatophytes, may throw much light on the origin of the seed and seed habit.

The living groups of the gymnosperms comprise in all less than 450 species, of which more than 300 are conifers and about 80 are cycads. With the exception of the conifers, these groups are hardly more than remnants of the ancient gymnosperm floras. But the conifers are a very successful group, which still forms extensive forests in some temperate regions and covers mountain sides and certain large rather barren areas, although such forests are being rapidly cut off for timber. Of the smaller groups the cycads are mostly tropical, the *Ephedras* are chiefly desert plants, and the *Gnetums* tropical vines with large-veined leaves. Like the horsetails and club mosses, the *Ephedras* have for the most part developed peculiar life habits under unfavorable conditions, and so have been able to avoid total extinction by withdrawing as far as possible from competition with the more recent floras.

This account can only consider the two largest groups, the cycads and the conifers.

The Cycads

346. The cycads. The cycads (order *Cycadales*) have thick stems which rarely branch and are generally rather short, resembling immense tubers partly buried in the ground (Fig. 293, *A*).



A, plant bearing a carpellate cone. *B*, a carpel in side view, showing the two very large ovules: *m*, mycropyle. — *A*, adapted from a photograph by Land

Fig. 293. A cycad (*Zamia*)

Some of the cycads have, however, stems which rise like columns ten to forty feet high. The compound leaves, like immense stiff feathers, form a crown at the top of the stem so that the general habit of the cycads is somewhat like that of the tree ferns and palms. One form (*Cycas revoluta*), incorrectly called the sago palm (since it is not a palm), is valuable for the sago of commerce which is obtained from the stem.

347. The cones of the cycads. Some of the cycads bear cones composed either of carpels (megasporophylls), or stamens (microsporophylls) which resemble large scales. Carpellate and staminate cones are always borne on separate plants. In other types, however, as *Cycas revoluta*, the carpels, especially, have more nearly the appearance of vegetative leaves (Fig. 294), and form rosettes at the top of the stems. *Cycas revoluta* is frequently grown in park conservatories, and occasionally produces these rosettes of hairy, orange-colored carpels, which bear a series of ovules as large as plums on either side. Well-differentiated cones are present in *Zamia* (Fig. 293, *A*), which is quite common in southern Florida.* The carpel (Fig. 293, *B*), in this genus, bears two ovules and the stamen, a group of pollen sacs (Fig. 295, *A*). The ovule (Fig. 295, *D*) has a thick integument surrounding the large nucellus, in which lies the embryo sac containing the female gametophyte. The pollen grains of *Zamia* enter the opening called the *micropyle* (meaning little gate), where the integument fails entirely to inclose the nucellus, and so come to lie in a small cavity

FIG. 294. Carpel of *Cycas revoluta* bearing five ovules

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* TO THE INSTRUCTOR: It ought to be possible to obtain *Zamia* in quantities for advanced classes. The type is most admirable for the study of the gametophytes of gymnosperms. The best account of these is given by Webber, United States Department of Agriculture, Bureau of Plant Industry, *Bulletin 2*. 1901.

termed the *pollen chamber* (Fig. 295, *D, p*). The pollen grains germinate in the pollen chamber, forming male gametophytes, whose development disorganizes much of the tissue at the tip of the nucellus, so that the pollen grain end of the male gametophytes finally hang down just above the embryo sac.

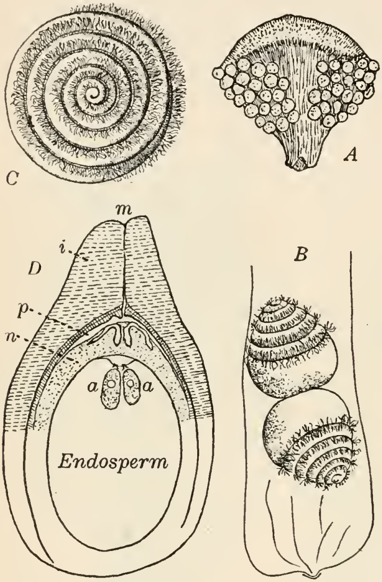

FIG. 295. The sperms and ovule of a cycad (*Zamia*)

A, lower surface of a stamen, with numerous pollen sacs in two groups. *B*, the two large top-shaped motile sperms at the end of the pollen tube ready to be discharged above the archegonia. *C*, a sperm viewed from the end, showing the spiral band which bears the cilia. *D*, diagram of a section of an ovule after pollination: *m*, micropyle; *i*, integument; *p*, pollen chamber; *n*, nucellus containing developing pollen tubes; *a*, archegonia, with large eggs imbedded in the endosperm (female gametophyte). — *B*, *C*, after Webber

348. The gametophytes of the cycads. The embryo sac of the cycads is said to develop from one of a group of four cells in the interior of the nucellus. Such a group is undoubtedly a tetrad, and each of the four cells corresponds to a megaspore, but only one produces a female gametophyte, and thus becomes an embryo sac.

The nucleus of the embryo sac (megaspore nucleus) gives rise to a great many hundred nuclei, and the amount of protoplasm increases very greatly until the embryo sac occupies the larger part of the interior of the nucellus in this large ovule. The nuclei at first lie freely in the protoplasm, but, later, walls are formed and the embryo sac becomes filled with a delicate tissue, called the *endosperm* (Fig. 295, *D*), which corresponds to the vegetative part of a prothallium in a fern. Several archegonia are developed at the micropylar end of the endosperm (Fig. 295, *D, a*). These are very much reduced in structure, the neck being represented probably by two small cells and the very large eggs lying imbedded in the cells of the endosperm.

The male gametophyte consists of the protoplasm with several nuclei contained in the pollen grain and tube. Some of the nuclei near the pollen grain end of the tube lie within delicate cell walls. One of these cells termed the *generative cell* develops two sperm mother cells which become organized into two very large *motile sperms* (Fig. 295, *B, C*), each with a spiral band or line bearing hundreds of cilia. The two sperms finally begin to move around in the fluid of the pollen tube and are discharged from the end nearest the pollen grain (which now hangs down over the embryo sac) into the fluid within the cavity formed from the disorganized tissue at the tip of the nucellus. The pollen tube in the cycads grows off to one side in the nucellus and seems to be a sort of absorbing organ, so that it does not carry the sperms to the embryo sac as the sperm nuclei are carried in most seed plants.

The motile sperms are set free in the fluid above the embryo sac, whose female gametophyte at that time bears mature archegonia. They have been observed swimming about for many minutes in sections of the living ovules, and probably have a long motile period in the ovule. One of them is finally able to enter the neck of an archegonium, and fusing with an egg fertilizes it.

The finding of motile sperms in the cycads and in *Ginkgo*[1] by two Japanese botanists in 1896–1897 proved two of the most interesting botanical discoveries of the past decade. It is very remarkable that the sperm-forming habits of the bryophytes and pteridophytes should have persisted so long after the seed habit became established in a group. The free swimming of these motile sperms is actually a return, such as occurs in the bryophytes and pteridophytes, for a short time in the life history of the cycad to the aquatic habits of an algal ancestry of ages ago.

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[1] A beautiful Japanese tree, not uncommon under cultivation.

The Conifers

349. The conifers. This group (order *Coniferales*) has representatives distributed all over the earth, some of them forming the most extensive forests and having the greatest value as timber trees. There are not many more than 300 species of conifers, of which the pines (*Pinus*) have 70; *Podocarpus* (growing in South America and eastern Asia), 40; the junipers (*Juniperus*), 30; certain cedars (*Cupressus*), 20; the firs (*Abies*), 20; and the spruces (*Picea*), 12. Others have few species and a very limited distribution. Such a form is the giant redwood of California (*Sequoia gigantea*), which is found only in a few scattered groves in the Sierra Nevada Mountains (Fig. 33).

350. The form and foliage of the conifers. The form and foliage of the conifers is generally very characteristic. The trees have, as a rule, a single central stem which rises vertically from the ground, and the side branches spread out horizontally from this shaft so that the trees are very symmetrical and taper to a point like a cone. The foliage, as a rule, consists of scale- or needle-shaped leaves, which usually remain on the trees for a number of years so that most of the trees are evergreen. But there are some exceptions to the rule, as the larch or tamarack (*Larix*), which sheds its needles every year.

The needle leaves can endure severe cold, fierce heat, and drought. This is made possible by their very compact structure (Fig. 296), which presents a minimum of surface exposure and the protective layer of thick-walled cells under the heavy epidermis. The chlorophyll-bearing tissue is closely packed in the pine leaf and consists of cells with peculiar infolding walls. Some species of pine have needles with one fibro-vascular bundle, e.g. the white pine; others have two bundles, e.g. the Scotch and the Austrian pine. The buds, leaves, and stems contain much resin and turpentine, which render them unpalatable to grazing animals and cover them with a film which sheds water and protects the plant both from the winter's cold and the summer's drought. Resins and turpentines are also very effective in protecting young conifers from the attacks of parasitic fungi, especially when the trees are wounded.

Certain pines furnish the resin and turpentine of commerce. Incisions are made through the bark, penetrating the wood. A thick liquid oozes out which is a mixture of resins and oil of turpentine. This liquid is then distilled, driving off the fluid oil of turpentine which is collected. The resin remains behind in the still, and when cool is no longer semi-fluid, but becomes quite hard and brittle. The timber value of certain conifers is much greater than that of most other kinds of trees because the wood is soft, splits regularly, is easily worked, and also because the tree trunks are so straight. The problems of forestry (see Chapter XLI) are largely concerned with the preservation of the pine forests, which are being cut off with little regard to the future.

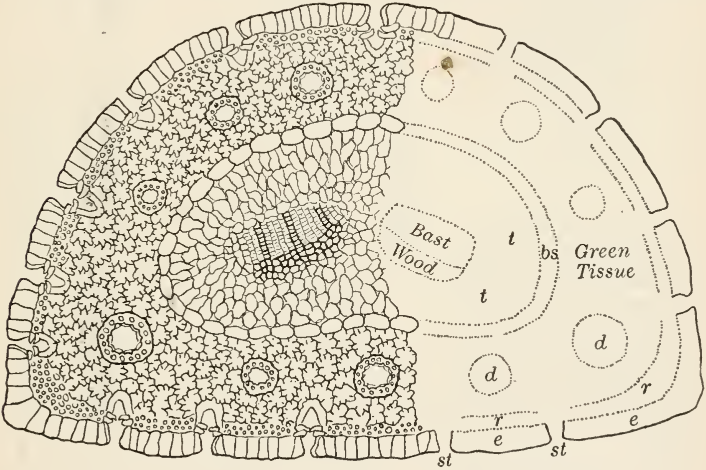

Fig. 296. Structure of a pine needle (*Pinus Laricio*)

The compact green tissue, or mesophyll, with resin ducts *d*, surrounds an area containing two fibro-vascular bundles, which lie in a peculiar region of transfusion tissue *t*, bounded by the bundle sheath *bs*. Outside of the green tissue are thick-walled cells forming a rigid tissue *r*, and around the whole is the heavy epidermis *e* with lengthwise grooves containing the stomata *st*

351. The tissues of the pine stem. The pine is an excellent subject for the study of stem structure and growth in a timber tree. There are five principal regions in the stem: (1) the *pith*, (2) the *wood*, (3) the *cambium*, (4) the *bast*, and (5) the outer *bark* (see Fig. 297, *B*).

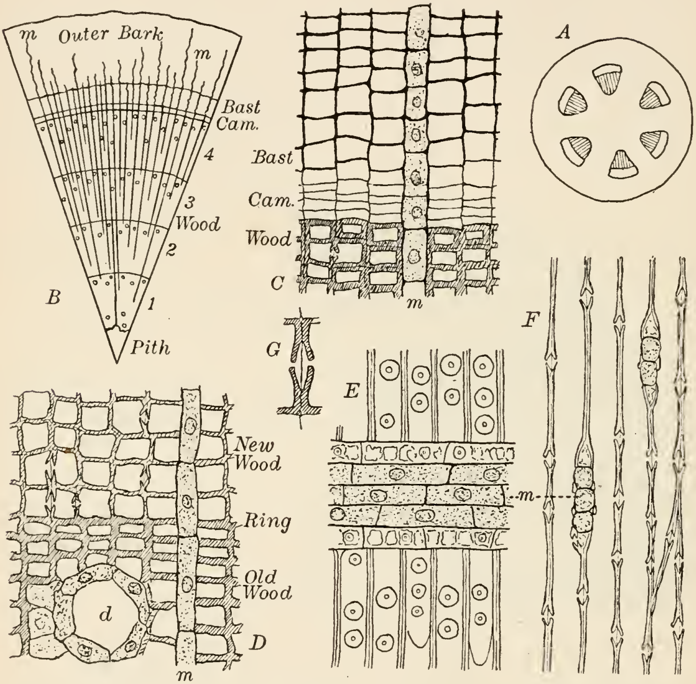

Fig. 297. Structure of the stem of the Scotch pine (*Pinus sylvestris*)

A, diagram of the arrangement of the fibro-vascular bundles at a growing point: the shaded parts are wood. *B*, diagram of the position of the principal tissues shown in a cross section of a four-year-old stem. *C*, cross section of a region of cambium *Cam*, with adjacent wood and bast. *D*, cross section of wood at an annual ring: *d*, resin duct. *E*, radial section of wood. *F*, longitudinal section of wood. *G*, section of bordered pit. Medullary rays *m* appear in most of the figures

The *pith* occupies the very center of the stem, and is the remains of the undifferentiated primitive tissue present at its growing point before the fibro-vascular bundles and bark are formed. It practically disappears as the stem grows older and the wood increases by a number of years of annual growth.

The *wood*, or *xylem*, comprises by far the greater part of older stems, becoming proportionally greater as each annual ring is added. It is composed of very much elongated cells, called *tracheids*, with firm, somewhat yellowish, thick walls. Cell walls of this character are said to be *lignified*. These cells contain pits (Fig. 297, *E, F, G*) surrounded by a circle and termed bordered pits, the circle being a feature characteristic of this group of plants. There are resin ducts among the wood cells, and also peculiar plates of cells called *medullary rays* which extend through the cambium and bast into the outer wood. The medullary rays have the form of thin knife blades penetrating the wood for various distances.

The *cambium* is a cylinder of thin-walled cells just outside of the wood, and is the most active region of growth in the stem. This cylinder (Fig. 297, *C*) is only two or three cells wide, and the cells are continually dividing by walls parallel to the surface (tangentially) during the season of growth. The daughter cells on the inside of the cambium become firm wood cells by the thickening of their walls together with certain changes (lignification) that give them firmness; they also become empty of protoplasm. The daughter cells on the outside of the cambium form the bast, remaining soft and containing protoplasm and much food material. The cambium thus adds cells to the wood on the inside and the bast on the outside. The wood is deposited in annual rings during the season of growth, and these are sharply distinguished from one another because the wood cells formed at the beginning of one season are larger than those formed in the latter part of the previous season (Fig. 297, *D*).

The *bast* is difficult to study chiefly because the cells are under severe pressure from the growing cambium on the inside and the restraining bark on the outside, and the cell arrangements are frequently distorted.

The *outer bark* is developed from the primitive or ground tissue which lay outside of the circles of wood and bast when these circles were first formed by the union of the primary fibro-vascular bundles (Fig. 297, *A*), as described in Sec. 79. There is much actively growing tissue in the bark, but the outer regions become quite dead, and crack under the pressure of the growing cambium, thus forming scales. The cracks are healed by the living tissue of the bark. The bast is generally so closely attached to the outer bark that it peels off with it, and therefore

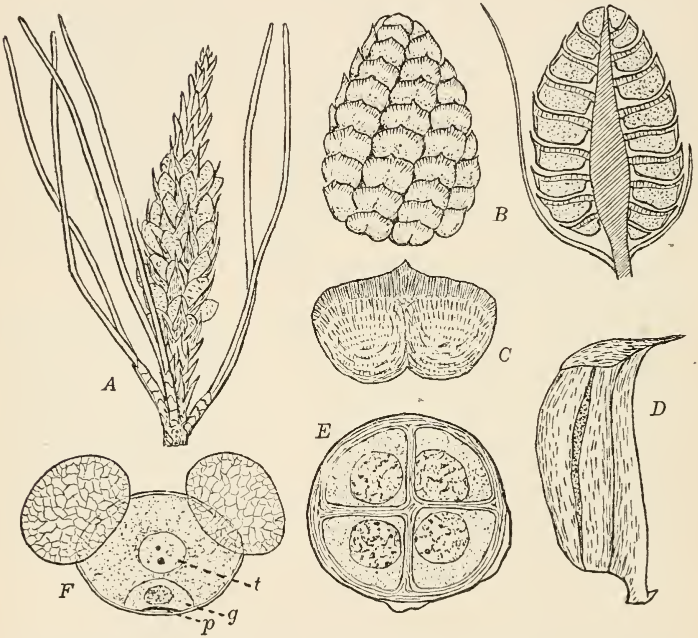

Fig. 298. The staminate cone, stamen, and pollen of the Scotch pine (*Pinus sylvestris*)

A, young growth, with staminate cones about two weeks after the opening of the terminal bud. *B*, details of cone. *C*, end view of stamen. *D*, side view of stamen. *E*, pollen mother cell developing four pollen grains in a tetrad. *F*, pollen grain showing the two wings: *p*, prothallial cell; *g*, generative cell; *t*, tube nucleus. — *E*, after Miss Ferguson is a sort of inner bark and must be included in any account of this region of the stem.

The functions of these tissues are discussed in Part I, Chapter VIII.

352. The cones of the pine. The cones of the pine, as in all conifers, are of two sorts: (1) *staminate*, when made up of *stamens* (microsporophylls), and (2) *carpellate*, when composed of *carpels* (megasporophylls).

The staminate cone. The staminate cones are developed in clusters on the young growth that appears late in the spring with the opening of the terminal buds (Fig. 298, *A*). Each cone consists of a large number of stamens closely packed together and arranged somewhat spirally around the central axis (Fig. 298, *B*). The stamen bears two pollen sacs (Fig. 298, *C*, *D*), within which the pollen grains are developed. The pollen grains are formed in groups of four, or tetrads (Fig. 298, *E*), just like the spores of the bryophytes and pteridophytes, and their further history shows them to correspond exactly to the microspores.[1] The pollen sac is then a microsporangium, and the stamen a microsporophyll. The pollen sacs develop from a group or region of cells as in the horsetails, lycopods, and *Selaginella*, and not from a single surface cell as in the common ferns.

The pollen grains are produced in enormous quantities, and being set free by the splitting of the pollen sacs, they are scattered as fine yellow dust by the wind. Sometimes pollen is carried from pine forests by the wind for many miles, falling as so-called showers of sulphur. The pollen grains are especially adapted for distribution by the wind, for the outer layer of the cell wall is swollen on two sides to form outstanding wings (Fig. 298, *F*).

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[1] This relationship is further established by the count of the chromosomes in the Scotch pine (*Pinus sylvestris*), which shows that the pollen grain has 12, while certain tissues of the pine sporophyte have 24. Pollen formation is then the period of chromosome reduction when the sporophyte generation passes over to the gametophyte, as explained in Secs. 334 and 335. Similar chromosome reduction undoubtedly takes place with the formation of the embryo sac in the nucellus.

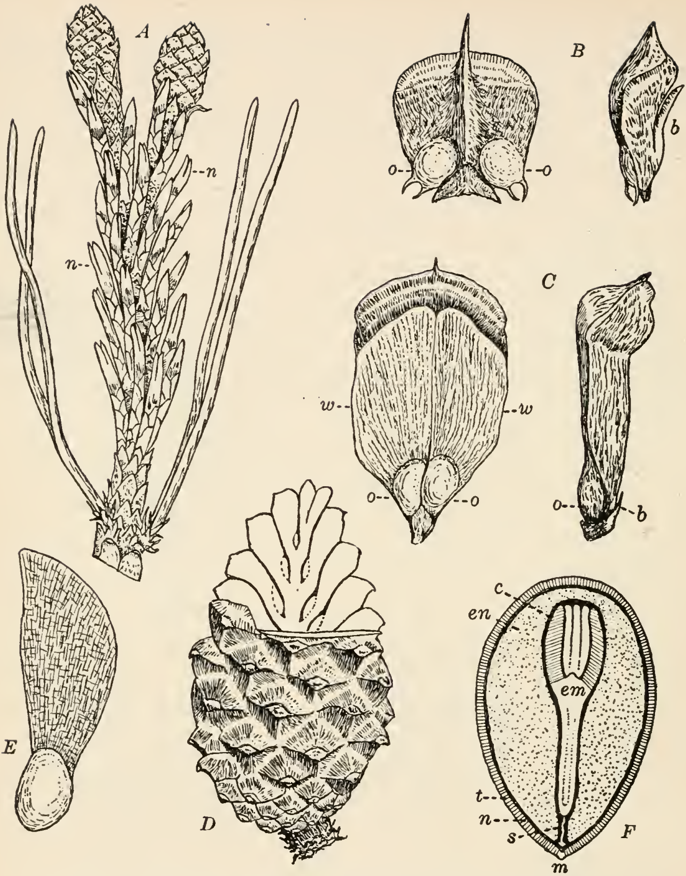

FIG. 299. Carpellate cone, carpels, and seed of the Scotch pine (*Pinus sylvestris*)

A, young growth with carpellate cones, about three weeks after the opening of the terminal bud: *n*, young pine needles. *B*, inner and side view of a cone scale at the time of pollination as shown in *A*: *b*, bract; *o*, ovules. *C*, inner and side view of scales from a two-year-old cone as shown in *D*: *b*, bract; *o*, fertilized ovules now rapidly maturing into winged seeds; *w*, the developing wings. *D*, a two-year-old cone. *E*, a mature winged seed. *F*, section of mature seed: *t*, hard seed coat, or testa, developed from the integument of the ovule (see Fig. 300, *A*, *i*); *n*, a membranous seed coat which is the remains of the nucellus (see Fig. 300, *A*, *n*); *en*, endosperm or tissue of the female gametophyte (see Fig. 300, *A*); *em*, embryo with group of cotyledons *c* and the suspensor *s*; *m*, micropylar end of seed

The carpellate cone. The carpellate cones have a complex structure that cannot here be described in detail. They are borne singly or in groups of two or three at the ends of the new growth in the spring (Fig. 299, *A*) simultaneously with the staminate cones. Each cone is composed of scales arranged somewhat spirally. Each scale (Fig. 299, *B*) is believed to be a group of three fused carpels (the point representing a sterile carpel between two fertile ones). The scale bears a pair of ovules below on the inner face, near the place where it is attached to the axis of the cone.

The ovule has a large nucellus, surrounded by an integument, which bears two appendages looking like a pair of horns in miniature (Fig. 299, *B*, *o*). The embryo sac which develops in the center of the nucellus is one of a group of four cells, or tetrad, which shows its relationship to a spore (megaspore) and to the pollen grain. The other three cells of the tetrad fail to develop, so that all the strength of the ovule is given to this single functional megaspore which produces the female gametophyte. The ovule is an outgrowth from the surface of the carpel, its nucellus (Fig. 300 *A*, *n*) corresponds to a megasporangium, and the integuments (Fig. 300, *A*, *i*) are probably protective investments. The integuments do not completely inclose the nucellus, but there is left a small opening at the tip (Fig. 300, *A*, *m*) called the micropyle.

353. Pollination in the pine. The young carpellate cones are upright when they first appear, and the scales are slightly separated from one another. When the pollen is shed in clouds from the stamens some of the grains are carried by the wind to the carpellate cones and sift in between the scales, collecting in little drifts near the ovules. This is the process of *pollination.* At this time there are globules of moisture between the two hornlike appendages of the ovules, and the pollen grains are caught by these. The fluid gradually dries up, drawing the pollen grains toward the micropyle, and finally into a cavity called the *pollen chamber* (Fig. 300, *A*, *p c*), which lies just above the nucellus.

Meanwhile the scales of the cone close together and the cone bends over until it hangs downward. This is a curious behavior, although there is evident advantage to the plant, for the cone is now in a better position to protect the ovules from rain or dust which might enter between the scales if the cones remained upright.

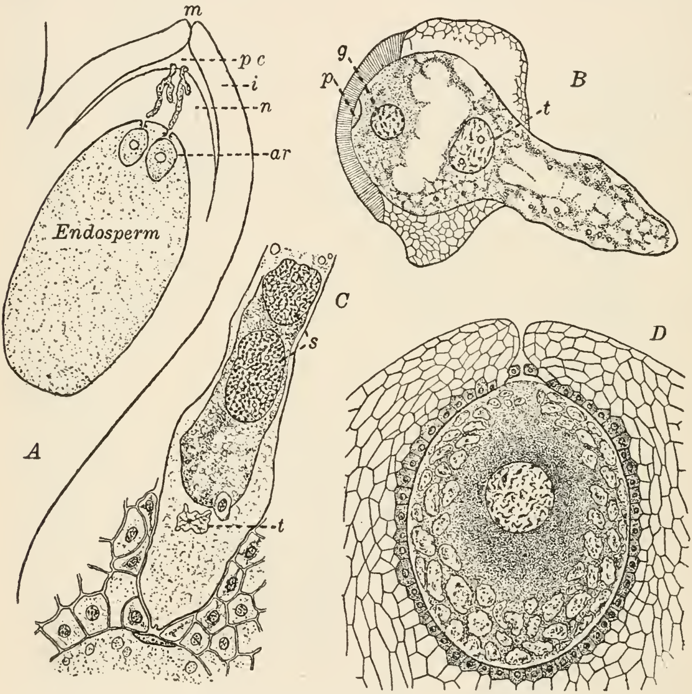

Fig. 300. The gametophytes of the pine

A, diagram of a section of a year-old ovule: embryo sac with mature archegonia *ar* imbedded in the tissue of the *endosperm* (female gametophyte); pollen tubes (male gametophytes) growing down through the tissue of the nucellus *n*; *p c*, pollen chamber; *m*, micropyle; *i*, integument. *B*, germinating pollen grain, showing young male gametophyte: *t*, tube nucleus; *g*, generative nucleus; *p*, prothallial cell. *C*, tip of pollen tube applied to the egg: *t*, tube nucleus; *s*, the two sperm nuclei. *D*, a mature archegonium sunken in the tissue of the endosperm, showing the large egg surrounded by a jacket of cells rich in protoplasm: two neck cells of the archegonium shown just above the egg. — *B*, *C*, after Miss Ferguson

354. The gametophytes of the pine. The pine, like all seed plants, is of course heterosporous because it has microspores (pollen grains) and megaspores (embryo sacs); so there are two gametophytes, male and female.

The male gametophyte. The male gametophyte, as in most, if not all, seed plants, begins to develop before the pollen is shed. There are three nuclear divisions which cut off two small cells, called *prothallial cells,* of which traces may sometimes be found against the wall of the pollen grain (Figs. 298, *F, p*; 300, *B, p*). The third division leaves the pollen grain with a nucleus (the tube nucleus) in the central region and a small lens-shaped cell (the generative cell) at one side (Fig. 298. *F, g*). This is the condition when the pollen is shed.

Shortly after pollination the pollen tubes begin to develop in the pollen chamber (Fig. 300, *A, p c*), but their development is very slow until the following spring. Then the large tube nucleus passes to the tip of the tube, which grows rapidly towards the center of the nucellus (disorganizing the surrounding tissue as it does so), where the female gametophyte lies within the embryo sac. The generative cell now divides into a stalk and body cell which pass into the tube. The body cell forms two sperm nuclei a few weeks later. Four nuclei are then finally present at the end of the pollen tube (two sperm nuclei, the tube nucleus, and that of the stalk cell). The pollen tube has now reached the embryo sac and is ready to discharge its contents into one of the eggs developed by the gametophyte (Fig. 300, *D*).

The female gametophyte. The embryo sac (megaspore) is a one-nucleate cell at about the time of pollination. This nucleus gives rise by repeated divisions to a large number of nuclei that lie at first freely in the protoplasm as the embryo sac gradually increases in size. Later, cell walls are formed around the free nuclei, and the entire embryo sac becomes filled with a delicate tissue called the *endosperm* (Fig. 300, *A*), which corresponds to the vegetative portion of a prothallium. It takes almost a full year for the female gametophyte to reach this stage of development, when it occupies the greater part of the nucellus. In the spring following the pollination of the cone, the endosperm forms a group of several archegonia at its micropylar end. Each archegonium (Fig. 300, *D*) consists of a much-reduced neck region, generally composed of four cells, and the very large egg which lies imbedded in the endosperm, whose cells form an investment around it called the *jacket*. The egg is filled with dense protoplasm and contains much food material supplied through the cells of the jacket.

This is the condition of the female gametophyte thirteen months after pollination. At about this time the pollen tube reaches the embryo sac and entering it passes between the neck cells of an archegonium, where its tip fuses with the egg membrane. The contents at the end of the pollen tube are discharged into the egg, including not only the two sperm nuclei, but also the tube nucleus and that of the stalk cell. One of the sperm nuclei moves towards the egg nucleus, which lies near the center of the egg, and fusing with it completes the act of *fertilization*. The other three nuclei break down and soon disappear.

355. The development of the embryo in the pine. Fertilization takes place, as described above, a little more than a year after pollination. The cone during this time has increased greatly in size, but is generally hardly a third as large as the mature seed-bearing cone.

The fertilized egg soon begins to develop the pine embryo. This is a complicated history, which cannot be described here in detail. The embryo is however formed at the end of a structure called the *suspensor* (Fig. 299, *F*, *s*), whose development carries the embryo into the center of the endosperm, where it lies in a favorable situation for its nourishment. The embryo (Fig. 299, *F*, *em*) is straight, and the stem part is surrounded by a circle of seed leaves called *cotyledons*. The pine seedling is shown in Fig. 12.

Meanwhile the integument becomes firmer and finally forms the hard, protective seed coat, or *testa* (Fig. 299, *F, t*). Adjacent tissue of the cone scale above the ovule develops a membranous wing (Fig. 299, *C, w*), which separates from the scale of the cone with the ovule as a part of the seed. It takes another full year for these changes to take place, and the cone is not fully mature (Fig. 299, *D*) and the seeds ripe until somewhat more than two years after pollination. Then the scales of the cone, now quite woody in texture, separate, and the seeds are shaken out, and since they are winged (Fig. 299, *E*) they may be carried for a considerable distance by the wind.

356. The life history of a gymnosperm. The life history of a gymnosperm, beginning with the sporophyte (for the gametophyte phases are now so inconspicuous that they only appear during the process of seed formation), may be formulated as follows:

$$\textit{Sporophyte} < \begin{array}{l} \underset{(\textit{microspore})}{\textit{pollen grain}} - \underset{(\textit{protoplasmic contents of pollen tube})}{\textit{Male Gametophyte}} - \textit{sperm nucleus} \\ \underset{(\textit{megaspore})}{\textit{embryo sac}} - \underset{(\textit{protoplasmic contents of embryo sac})}{\textit{Female Gametophyte}} - \textit{egg} \end{array} > - \textit{Sporophyte}, \text{ etc.}$$

This in abbreviated form becomes

$$S < \begin{array}{c} p\,g - M\;G - s \\ e\,s - Fe\;G - e \end{array} > - S, \text{ etc.}$$

This formula should be compared with that of some heterosporous pteridophyte, as *Selaginella* (Sec. 326), to make clear the relationships. When carefully studied it will be found to be merely an elaborated form of the simple formula of alternation of generations.

$$G < \begin{smallmatrix} s \\ e \end{smallmatrix} > - S - sp - G < \begin{smallmatrix} s \\ e \end{smallmatrix} > - S - sp - G, \text{ etc.}$$

The peculiarities of the life history of a gymnosperm are due to heterospory (and this is true of all seed plants), by means of which two sexual plants, male and female, have been differentiated, and the fact that both gametophytes live wholly or almost wholly as parasites upon the sporophyte.

SUBDIVISION II. THE ANGIOSPERMS, OR *ANGIOSPERMÆ*

357. The angiosperms. The angiosperms (meaning seeds in a vessel) are distinguished by the fact that the ovules are developed in a closed case (ovule case or ovary) formed by the carpels, sometimes alone but often together with adjacent tissue of the stem. This immense assemblage of plants, with more than 120,000 species, forms the greater part of the earth's vegetation and includes the most successful groups, dominating most of the land floras. It is a much more varied assemblage than the gymnosperms, and successful in every vegetation form (herb, shrub, or tree). The angiosperms adapt themselves to all sorts of life conditions, some of them being aquatics, others covering the meadows, prairies, and heaths, certain groups entering the deserts, and the trees forming forests generally accompanied by undergrowths of shrubs. They occupy the highest points of plant evolution, but along a great many very divergent lines, for some of the culminating groups are the grasses, the hardwood trees, the composite groups, the orchids, etc.

The general structure of the angiosperms, including the roots, stems, leaves, flowers, and fruits, together with many principles of plant physiology best illustrated in this group, have been described in Part I. This account will consider chiefly the life history, with especial reference to the gametophyte generations and significance of the flower.

358. The angiosperm flower. The essential structures of the angiosperm flower (Fig. 301), as of the gymnosperms, are the stamens (microsporophylls) and the carpels (megasporophylls); but in addition to these some accessory parts are generally present, which are either modified leaves of the plant, or sometimes stamens and carpels that have become sterile. These accessory parts constitute the *perianth* (Fig. 301, *p*), situated on the stem just below the stamens and carpels, and are generally showy structures, but also protective, at least in the bud. The perianth, as a rule, gives the characters of color and form which in popular usage define a flower. It is a very important accession, for it has resulted in some remarkable adaptations and devices on the part of the plant to insure pollination by the visits of insects (see Chapter XXXII). The structure of the perianth, with its parts, — *sepals* and *petals,* — is described in Chapter XIII. Besides having the perianth, the angiosperm flower is peculiar in that the ovules are not normally exposed on the surface of the carpels. This means that the carpels, either singly or in groups, form closed structures, which may be termed *ovule cases.* The ovule case, generally called the *ovary* (an unfortunate term, for it does not produce eggs but ovules), bears a receptive surface, termed the *stigma,* upon which the pollen grains may germinate. The stigma may be raised upon a stalk, or *style.* Ovule case, style, and stigma constitute the *pistil* (meaning a pestle), which is said to be simple when only a single carpel is involved, and compound if there is a group of carpels. The various arrangements of

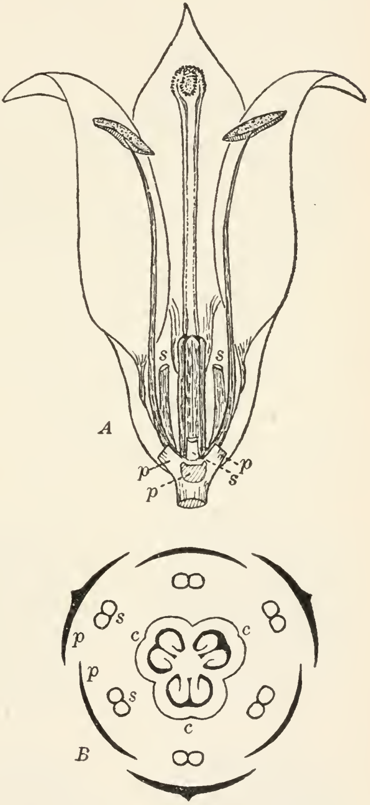

FIG. 301. The lily (*Lilium philadelphicum*)

A, dissected flower, showing the pistil and stamens: *p*, parts of the perianth which have been cut away; *s*, bases of stamens cut off. *B*, floral diagram: *p*, perianth, composed of two circles of similar and petal-like parts; *s*, stamens, likewise in two circles; section of ovule case (ovary) shown in the center, composed of three carpels (*c*) so united as to form three locules containing the ovules the carpels to form different types of pistils are described in Secs. 156 and 157.

Another characteristic of the angiosperm is the production of fruit. A fruit is a ripened ovule case, or ovary, frequently

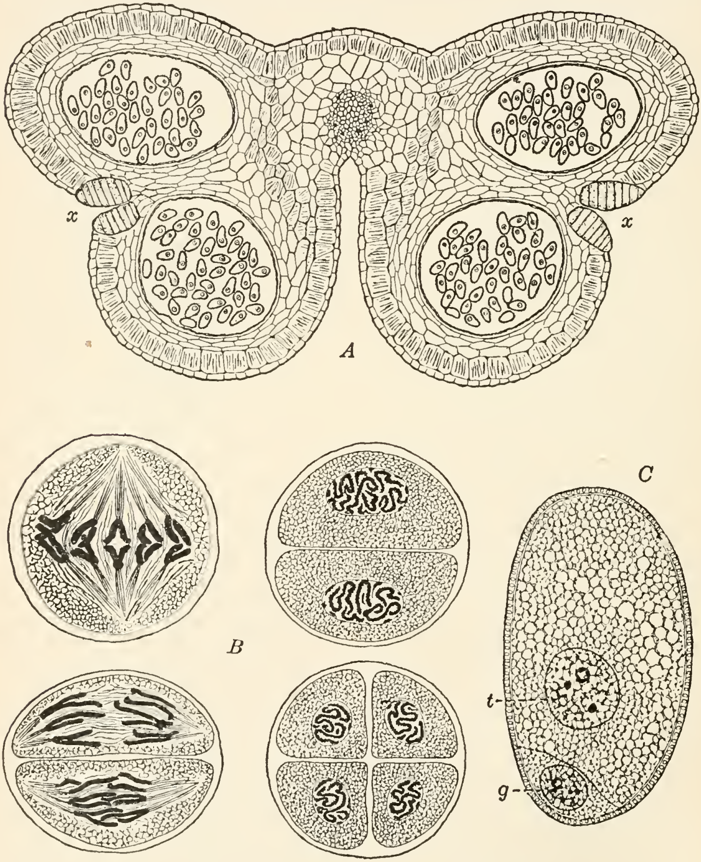

Fig. 302. Anther and pollen of the lily

A, mature anther, showing the four locules, or chambers, containing pollen grains: the anther opens lengthwise on both sides along the lines of cells shown at *x*. *B*, stages in the formation of pollen grains in a group of four (tetrad) within the pollen mother cell. *C*, mature pollen grain with early stages in the development of the male gametophyte: *t*, tube nucleus; *g*, generative nucleus with accessory parts. The gymnosperms do not have the exact equivalents of fruits, although the berry-like structures of the yew appear at first glance to be similar and the cone is, of course, a protective structure for the seeds. True fruits, as the term is used when applied to the angiosperms, are seed cases of various forms, — structures which are sometimes merely protective, and sometimes fleshy and attractive to animals for food. They are described in Chapter XVI.

The pistil distinguishes the angiosperms from the gymnosperms, and is a more important feature of the angiosperm flower than the perianth, which is frequently inconspicuous, and sometimes wholly or almost wholly absent. But the pistil in combination with a showy perianth of some peculiar and specialized form gives the highest types of flower structure. The most important of these are discussed in Chapter XIII. This account will only describe the stamens and carpels in their functions as spore-producing organs developing microspores (pollen) and megaspores (embryo sacs).

359. The stamen and the formation of pollen. The parts of a stamen are described in Secs. 171 to 173. Pollen formation takes place generally in four regions of the anther, which become *pollen sacs,* or *locules* (Fig. 302, *A*). The cells of these regions develop the pollen grains in groups of four, or tetrads (Fig. 302, *B*), and are consequently pollen mother cells. This process is identical with that of spore formation in the pteridophytes and bryophytes.[1] The pollen mother cell is a spore mother cell, and the pollen grain a spore, or more exactly a microspore.

The pollen sacs are sporangia, and like the sporangia of the horsetails, lycopods, *Selaginella*, and the pollen sacs of the

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[1] As in the case of the gymnosperms, the count of the chromosomes during pollen formation shows it to be a period of chromosome reduction, when the sporophyte generation passes over to the gametophyte, as explained in Secs. 334 and 335. Thus 24 chromosomes have been counted in various tissues of the lily plant, but only 12 appear in the nuclear divisions in the pollen mother cell (Fig. 302, *B*). These cells, it may be remarked, are exceedingly good subjects for the study of nuclear division.

gymnosperms (Sec. 352), they develop from a group or large region of cells, and not from a single surface cell as in the sporangium of the common ferns. The pollen sacs open along certain lines (Fig. 302, *x*) or by pores, and the pollen is thus set free. The pollen is carried in various ways to the stigma of the pistil, as described in Chapter XXXII, and its application to this structure constitutes pollination in the angiosperms. Wind, direct contact of the anthers with the stigma, or the visits of insects are means by which pollination is effected in this group of plants.

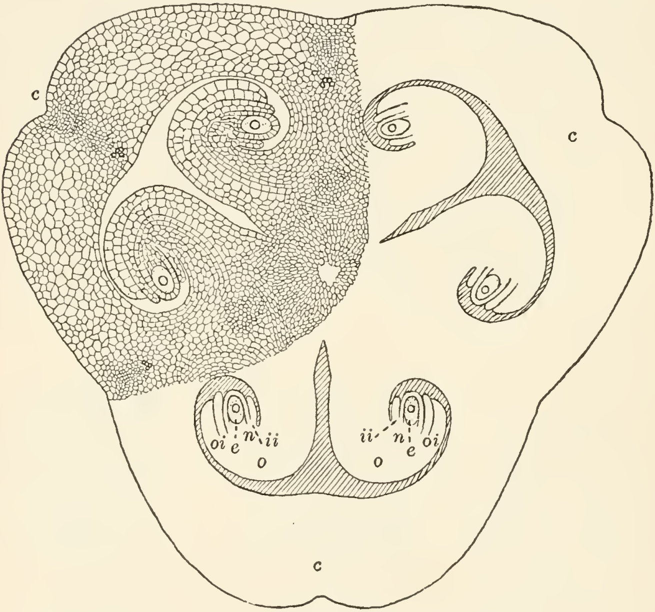

FIG. 303. Section of the ovule case (ovary) of the lily

Diagram of a cross section of a young ovule case, showing the three carpels *c*; each young ovule *o* has a large embryo sac mother cell *e* within the small nucellus *n*, and shows the developing inner and outer integuments *ii* and *oi*

360. The carpel and the formation of the ovule. The ovules are developed as outgrowths from the surface of the carpels (Fig. 303), or in some cases from regions of the stem, when this structure enters into the formation of the ovule case. Each ovule consists of a central region called the *nucellus* (Figs. 303; 306, *A*; 309, *A*, *n*), which becomes enveloped by two protective integuments (Figs. 303; 306, *A*; 309, *A*, *B*, *C*, *ii*, *oi*) that arise from its base and grow up around it, forming a small opening above termed the *micropyle* (meaning little gate). A cell in the interior of the nucellus becomes the *embryo sac* (Figs. 303, *e*; 306, *A*, *B*), which in most cases is the exact equivalent of a megaspore. This is proved by the fact that the embryo sac in such forms is one of a group of four cells, or tetrad (Fig. 304), and that the development of this group follows the same history as in pollen and spore formation. The nucellus is therefore a megasporangium. Certain forms of angiosperms, as the lily, have given up the formation of tetrads, and the spore mother cell develops directly into the embryo sac.[1]

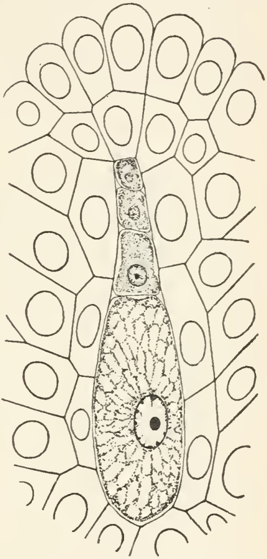
Fig. 304. A group of four megaspores (tetrad) in the nucellus of an ovule (*Canna*)

The upper three megaspores of the group are breaking down, while the lower is rapidly enlarging to become the embryo sac. — After Wiegand

361. The gametophytes of an angiosperm. The male gametophyte (contents of the pollen grain and tube) is clearly similar to that of the gymnosperm; but the female gametophyte of the angiosperm is a very much more reduced structure than anything in the gymnosperms.

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[1] In these cases the first two nuclear divisions within the embryo sac have the peculiarities of those in all spore mother cells. In the lily the nuclei of the nucellus have 24 chromosomes, but the nuclei of the embryo sac have 12. This shows that the two nuclear divisions characteristic of spore formation have become a part of the gametophyte phase of the plant's life history.

The male gametophyte. As in the gymnosperms, the male gametophyte begins its history in the pollen grain before the latter has been shed. The first division forms a *tube nucleus* and a *generative cell* (Fig. 302, *C*). The nucleus of the generative cell divides sooner or later to form two *sperm nuclei.* These three nuclei, with the rest of the protoplasm, constitute all there is of the male gametophyte (Fig. 305).

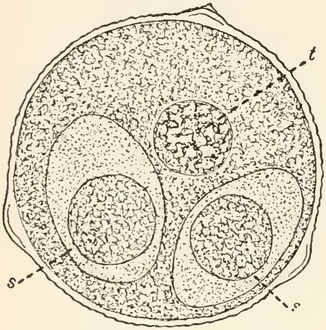

Fig. 305. Pollen grain of the elder (*Sambucus*)

The two sperm cells *s* and the tube nucleus *t*, with the remaining protoplasm, constitute the entire male gametophyte

The pollen grains germinate on the stigma of the pistil, finding there suitable fluids to start their growth. Each puts forth a tube (Fig. 156, *A*, *B*, *C*) which penetrates the stigma and grows downward toward the ovule case (ovary). The tube nucleus and the generative cell (or the two sperm nuclei if already formed) enter the tube and, passing to the tip, accompany its growth (Fig. 156, *D*, *E*, *F*).

The pollen tubes grow through the tissues of the stigma and style (if present) frequently over definite paths and enter the micropyles of the ovules. This behavior resembles the way in which parasitic fungi grow through the tissues of their hosts, and it is clear that the pollen tubes live largely or wholly parasitically on the sporophyte. On entering an ovule the pollen tube penetrates the nucellus and grows toward the embryo sac, which by this time has developed the female gametophyte.

The female gametophyte. The mature female gametophyte of an angiosperm (Fig. 306, *B*) contains only eight nuclei, the products of three nuclear divisions in the embryo sac. These are distributed as follows: There is a group of three nuclei at the micropylar end of the embryo sac (Fig. 306, *B*, *m*), forming the *egg apparatus,* of which one, with surrounding protoplasm, constitutes the *egg,* and the other two are called *synergids* (meaning co-workers). There is a group of three nuclei at the opposite end of the sac, called *antipodal nuclei* (Fig. 306, *B, ant*), which frequently become inclosed by delicate walls and possibly represent a prothallial region. The remaining two nuclei, called *polar nuclei* (Fig. 306, *B, p*), pass from the opposite ends to the center of the embryo sac, where they later unite.

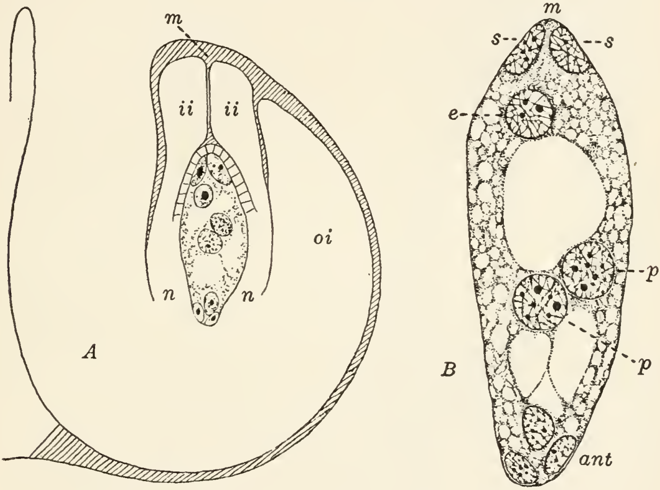

Fig. 306. The ovule and embryo sac of the lily

A, ovule with mature embryo sac: the inner integument *ii* has grown beyond the nucellus *n*; *oi*, outer integument; *m*, micropyle. *B*, mature embryo sac: egg apparatus at the micropylar end *m*; *e*, egg; *s*, synergids; the two polar nuclei *p* are about ready to fuse near the center of the sac; *ant*, antipodal nuclei

362. Fertilization and double fertilization. The tip of the pollen tube fuses with the end of the embryo sac, near the synergids, and the two sperm nuclei are discharged into the sac. The tube nucleus has generally broken down and disappeared entirely by this time (Fig. 156, *F, G*). One of the sperm nuclei unites with the egg nucleus (Fig. 307, *e, fs*), and this is the process of fertilization.

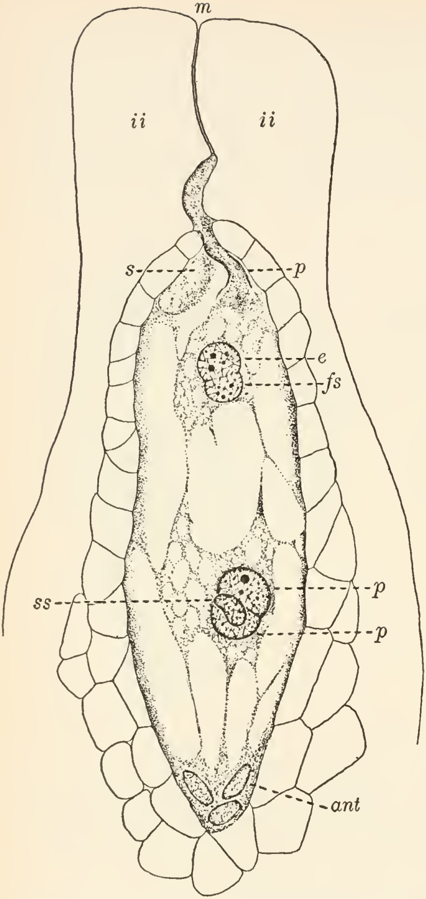

FIG. 307. Fertilization in the embryo sac of the lily

The first sperm nucleus *fs* fusing with the egg nucleus *e*; the second sperm nucleus *ss* is fusing with the two polar nuclei *p* near the center of the sac, constituting the so-called double fertilization; *p*, pollen tube; *s*, synergid breaking down; *ant*, antipodals; *ii*, inner integument; *m*, micropyle

The other sperm nucleus is known in a number of forms to pass to the center of the sac and unite with the two polar nuclei, constituting a triple fusion (Fig. 307, *p*, *p*, *ss*), and forming a large nucleus, called the *endosperm nucleus.* Since the endosperm nucleus has an important history in the development of the seed, this peculiar behavior of the second sperm nucleus is important, and it is called the double fertilization of the embryo sac.[1]

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[1] Double fertilization is probably the explanation of the phenomenon called *xenia*, which is the appearance at once in the seed of some character of the male parent. Thus a yellow or white kind of corn, when pollinated from a blue or red variety, will produce blue or red kernels. This color in the corn is present in the endosperm, and the character comes into the seed through the second sperm nucleus. For an account of xenia see Webber, "Xenia, or the Immediate Effect of Pollen in Maize," United States Department of Agriculture, Division of Vegetable Physiology and Pathology, *Bulletin 22*, 1900.

363. The development of the embryo and endosperm. The fertilized egg develops the embryo, but as in gymnosperms, there is generally a preliminary growth called the *suspensor* (Fig. 309, *D, E, H, s*), which carries the young embryo into the center of the sac. The endosperm nucleus begins to divide at once after its formation, by the triple fusion of the second sperm nucleus with the two polar nuclei (Fig. 307). It gives rise to a large number of nuclei, which become distributed in the protoplasm of the rapidly enlarging embryo sac (Figs. 308, *e*; 309, *H, e*). Later, walls begin to form around these endosperm nuclei, first in the outer regions of the embryo sac, and finally the whole sac becomes filled with a delicate tissue.

This tissue is called the *endosperm*, and the embryo becomes imbedded within it as in the pine. But this endosperm has, of course, a very different origin from that of the gymnosperms, and is a special development peculiar to the angiosperms. The group of antipodal cells possibly corresponds to the endosperm in the gymnosperms, and the egg apparatus has been regarded as a

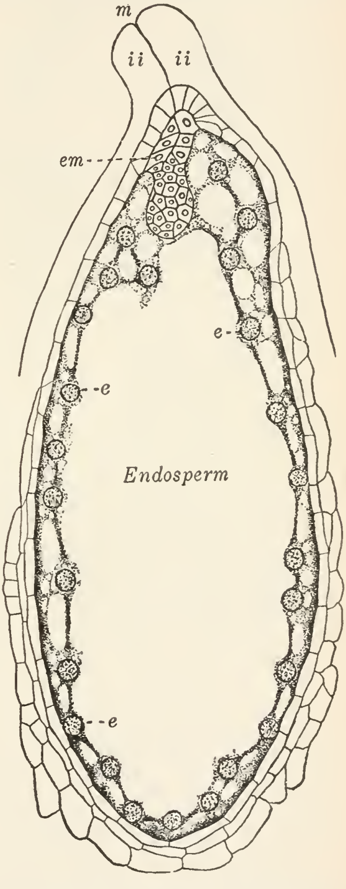

Fig. 308. Development of the embryo and the endosperm of the lily

The embryo *em* has developed from the fertilized egg; *e*, endosperm nuclei which have been derived from the triple-fusion nucleus, — that is, the two polar nuclei united with the second sperm nucleus (compare with Fig. 307); *ii*, inner integument; *m*, micropyle

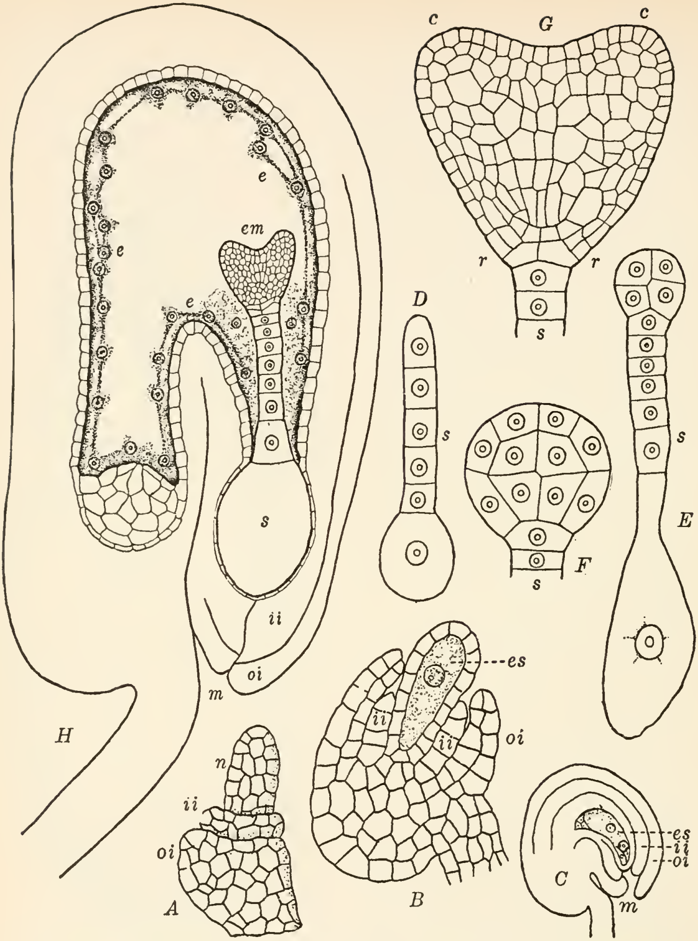

FIG. 309. Development of the ovule and embryo of the shepherd's purse (*Capsella*)

A, young ovule, showing origin of two integuments at base of nucellus *n*. *B*, outer integument growing beyond the inner, and the ovule beginning to bend over: *es*, embryo sac. *C*, diagram of a later stage with mature embryo sac. *D*, development of the suspensor *s*. *E*, early divisions of the terminal cell (embryo cell). *F*, later stage, showing the differentiation of an outer cell layer in the embryo, which is to become the epidermis. *G*, the two cotyledons *c* and the root region *r* now clearly defined. *H*, lengthwise section of an ovule, showing the position of an embryo in an embryo sac: *em*, embryo; *s*, suspensor; *e*, endosperm; *ii*, inner integuments; *oi*, outer integument; *m*, micropyle. — *A*, *B*, *C*, adapted after Campbell reduced archegonium. However, it is possible that all three of the nuclei in the egg apparatus represent eggs, only one of which is functional.

While the embryo and endosperm are developing, the ovule increases greatly in size, and its integuments change into the seed coats. In some plants, as in the squash (Fig. 1), peas, and beans, the embryo finally fills the entire seed, and the endosperm is almost completely crowded out, being represented by a thin membrane around the embryo. In other forms, as the corn (Fig. 3), asparagus, and poppy (Fig. 4), the embryos remain small, and the endosperm is conspicuous as a tissue richly stored with food material.

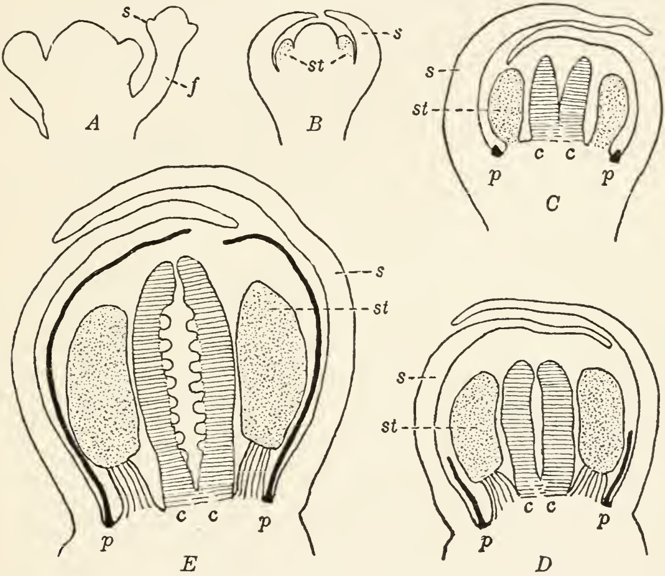

Fig. 310. Development of the flower of the shepherd's purse (*Capsella*)

A, tip of stem, showing the origin of the flowers: *s*, first appearance of the sepals in the flower *f*. *B*, sepals well along in their development and stamens *st* appearing. *C*, later stage, showing the two young carpels *c* and the beginnings of the petals *p*. *D*, later stage lettered as in the preceding. *E*, the petals now well developed, and the ovules beginning to arise on the inner face of the carpels, not yet united above to form the closed pistil

364. The development of the flower. The development of the parts of a flower would be expected to progress in the order of sepals, petals, stamens, and carpels, for this is, of course, the order of their position on the flower stalk, beginning from below. The parts of many flowers do arise in this order, but there are often irregularities due to the delayed appearance of some organs. For example, in the shepherd's purse the petals are formed last, arising between the sepals and carpels when the latter are far along in their development (Fig. 310, *C, p*).

The carpels are clearly separate in the beginning (Fig. 310, *C, D, c*), and the ovules at first may be exposed on their surface (Fig. 310, *E*), but sooner or later the carpels unite above, so that the ovules are finally contained in the ovule case (ovary).

A study of flower development makes clear the significance of perigyny and epigyny (Sec. 157), for it shows that the apparent fusion of parts, frequently called *coalescence,* when sepals, petals, or stamens seem to be united to one another or to the carpels (see diagrams, Fig. 136), is due to the formation of tubular outgrowths from zones of tissue below the floral parts. The parts which are most frequently affected by these zonal outgrowths are the carpels, and it seems probable that the compound pistil may have arisen from their activities. In many cases the ovules are developed from tissue that is probably really a part of the tip of the flower stalk.

365. The life history of an angiosperm. The formula for the life history of an angiosperm is the same as that of a gymnosperm (Sec. 356). The gametophyte phases, however, occupy generally a much shorter period, so that the seeds are matured in the same season and sometimes within a few weeks after pollination.

The formula is then as follows:

$$\textit{Sporophyte}\left\langle\begin{array}{ccccc} \textit{pollen grain} & - & \textit{Male Gametophyte} & - & \textit{sperm nucleus}\\ \text{(microspore)} & & \text{(protoplasmic contents of pollen tube)} & & \\ \textit{embryo sac} & - & \textit{Female Gametophyte} & - & \textit{egg}\\ \text{(megaspore)} & & \text{(protoplasmic contents of embryo sac)} & & \end{array}\right\rangle - \textit{Sporophyte,}\ \text{etc.}$$

THE ORIGIN OF SEED PLANTS AND THE SEED HABIT *

366. The origin of seed plants. We shall never know exactly when and how seed plants arose, for that important event in plant evolution probably took place earlier than the Carboniferous Age. We can, however, form some idea of the chief factors that brought about the seed habit from a study of the life histories of living pteridophytes and spermatophytes. As with a number of other forward steps in the evolution of plants, such as the origin of sex, alternation of generations, and heterospory, the seed habit probably was developed by a number of different groups of pteridophytes independently one of another. Thus the cycads and the conifers among the gymnosperms are so widely separated that it seems possible that they may have come from different pteridophyte parentage. Therefore the gymnosperms are generally regarded as a group of divergent evolutionary lines. The angiosperms are even more puzzling. Some botanists believe that they arose quite independently of the gymnosperms, but others hold that they may be distantly related to *Gnetum*. Some think that the monocotyledons and dicotyledons even have had independent origins. However, the view which seems to be finding greatest favor at present regards the monocotyledons not as the ancestors of the dicotyledons, but as derived from primitive dicotyledons.[1]

367. The origin of the seed habit. The most important factors leading to the seed habit appear to have been (1) *heterospory,* (2) *the retention of the megaspore in the megasporangium* to become the embryo sac in which the female gametophyte develops parasitically, and (3) *the development of the pollen tube* and its parasitic habit of growth through the tissues of the

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* To the Instructor: This subject is very difficult and may be omitted.

[1] These topics are far too technical for consideration here. For reviews of the various theories with their evidence, the reader is referred to Coulter and Chamberlain, *Morphology of Spermatophytes* (*Gymnosperms*), 1901 and *Morphology of Angiosperms*, 1903.

sporophyte to reach the embryo sac. These principles are associated with the last stages in the long processes of the evolution of the sporophyte and the degeneration of the gametophyte, which is briefly outlined in the next chapter.

Heterospory (Sec. 314, Chapter XXVII) has differentiated the spores of the pteridophytes and established male and female gametophytes, the first always developing from the microspores, and the second from the megaspores. At the same time the gametophytes became largely or wholly dependent upon food material stored in the spores, and smaller and simpler in their organization, until they degenerated into structures somewhat similar to those now illustrated in the heterosporous pteridophytes (*Marsilia*, *Selaginella*, *Isoetes*, etc.). Some of them finally lost all their chlorophyll, and adopted parasitic habits.

Heterospory also resulted in the differentiation of the spore leaves into microsporophylls and megasporophylls, and at last, as in many seed plants, the sporophytes themselves became differentiated, some producing only pollen (microspores) and some only embryo sacs (megaspores) in the ovules. In this way sexual characters of the gametophytes were gradually taken up first by the sporophylls and later by the sporophytes themselves, and thus the asexual generation began to assume the peculiarities of sex. The microsporophyll of the seed plant (stamen) took on characteristics of a male organ, and the megasporophyll (carpel) characteristics of a female one. The early botanists regarded the pollen grain as a male element and the stamen as a male organ, and it is true that these structures have male characters; but of course the actual male gametes are the sperm nuclei with closely associated protoplasm in the pollen tube whose contents represent a male gametophyte. And similarly, although the carpel has female characters, the female gamete is the egg within the embryo sac whose contents represent a female gametophyte.[1]

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[1] This subject is considered more at length in Chapter XXVII, Heterospory, Sec. 339.

The retention of the megaspore in the megasporangium was, perhaps, the most important step in the development of the seed habit. This retention was possibly at first somewhat accidental; that is, the megaspore simply failed to fall out of the megasporangium (as actually happens in some species of *Selaginella*, Sec. 325), and consequently developed its gametophytes while mechanically held on the sporophyte. Later the retention became more intimate and less mechanical, so that the female gametophyte established a close physiological association with the sporophyte, obtaining protection and certain foods, and perhaps most important of all it was kept moist. At last the megaspore, instead of being developed as a free cell, remained a part of the tissue of the megasporangium (nucellus of the ovule) and at that stage became the embryo sac with its clearly established parasitic relations to the sporophyte.

Some forms of *Selaginella* actually illustrate a beginning of such parasitic relations in the early stages of the development of its megaspore (Sec. 325), for the female gametophyte begins to develop before the spores are full grown and ready to be discharged. But the seed habit could not have been entirely formed until the megaspore became physiologically a part of the megasporangium, and the latter (as a nucellus), together with the protective integuments, became the ovule.

The development of the pollen tube is perhaps even more remarkable than the retention of the megaspore in the megasporangium. It seems clear that the pollen tube is a development in response to the stimulus of the moisture (containing food substances) which is excreted by the ovule in the gymnosperms and the stigma of the angiosperms. The habit may readily have had a very simple beginning if microspores fell into partially opened megasporangia, as indeed occurs in a species of *Selaginella* (Sec. 325), or among a group of megasporophylls. They would have found in such situations moisture and other conditions favorable for the development of outgrowths which later became tubes. These outgrowths and tubes would be expected to become more and more specialized as conditions arose which led to the final retention of the megaspore within the megasporangium, and at last they assumed pronounced parasitic habits.

With the parasitic habits of the pollen tube established it is not difficult to imagine the gradual adjustment of the peculiarities of pollination to those of ovule formation. It seems probable that the earliest forms of pollen tubes carried motile sperms to the embryo sac[1] (for motile sperms are even now present in the cycads and *Ginkgo*, Sec. 348), but later the complex structure of the sperm degenerated, with that of the whole male gametophyte, until the sperm nuclei became practically all that was left to represent the male gametes of the pteridophytes, bryophytes, and algæ. The simplification of the sperm and egg in the spermatophytes does not, however, affect the significance of these sexual elements, because it is known that the nuclei are the most essential structures of gametes.

Thus the peculiarities of the ovule and the pollen tube probably developed side by side, adjusting themselves to one another until the complex phenomena of pollination became established. These processes are relatively simple in the gymnosperms, where the pollen is applied directly to the ovule; but in the angiosperms a new feature was introduced when carpels, or groups of carpels, frequently with adjacent tissue of the stem, developed the ovule cases (ovaries). Yet it is not very difficult to understand how they may have arisen, for the same principles of protecting the megaspore (embryo sac) and providing for the germination

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[1] In certain fossil groups (*Pteridospermæ*), intermediate between the pteridophytes and spermatophytes, the evidence indicates that motile sperms were discharged into large pollen chambers filled with water, into which the necks of the archegonia opened so that the sperms were able to swim directly to the eggs. The pollen tube was probably at first an absorbing organ, or haustorium (as in the cycads and *Ginkgo* to-day, Sec. 348), penetrating the tissue of the ovule to obtain nourishment for the parasitic male gametophyte. Later, with the disappearance of the pollen chamber and motile sperms, the pollen tube took on the added function of carrying the sperm nuclei directly to the embryo sac.

of the pollen grains are simply carried one step farther, and the megasporophylls (carpels) become factors in the processes. Thus a receptive surface, the stigma, was developed as a special organ to receive and start the pollen tube in its parasitic development, which is to end with the fertilization of the egg.

The seed is the ripened ovule, for the principle of protection is continued after fertilization, and the integuments form hard seed coats, inclosing the developing embryo, supplied with food material by the parent sporophyte until it has reached an advanced stage of development.

THE EVOLUTION OF THE FLOWER

368. The evolution of the flower.* The higher types of flowers have been developed by long processes of evolution from the simpler structure of the primitive flowers. We do not know exactly what the primitive flowers were like, but some of their characters may be inferred from the structure of the simplest flowers of the angiosperms and the cones of gymnosperms and certain pteridophytes, as the horsetails and club mosses, which are truly flowers, if one accepts the definition of a flower as a "shoot beset with sporophylls." The most elaborately developed theory of floral evolution is that of Engler, and this brief outline will be a general statement of his views.

Primitive flowers were characterized by indefinite numbers of sporophylls, usually distributed in spirals, and the absence of the floral envelopes constituting a perianth. These conditions are illustrated in the cones of the pteridophytes and in many

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* To the Instructor: This subject should only be presented to classes with a fairly wide range of experience with flower structure in various groups of angiosperms. An excellent study would be a series of types from such an assemblage as the buttercup order, *Ranunculales*, as the mousetail (*Myosurus*), buttercups, magnolia, white water lilies, columbine, larkspur, aconite, etc., where many of the principles of flower evolution are illustrated in a single group. Similar studies might be planned for the rose order, *Rosales*, or the lily order, *Liliales*, followed by the orchids.

gymnosperms. Spiral arrangements of sporophylls (stamens and carpels) and floral envelopes are also not uncommon in many flowers with well-developed perianths, as in representatives of the buttercup order, *Ranunculales*, namely, mousetail (*Myosurus*), buttercups, magnolia, white water lilies, and the rose order, *Rosales*. It is not at all probable that the various advances over the primitive conditions followed any regular order. Some of them were concerned with *the differentiation of a perianth;* some had to do with *the arrangements of the sporophylls and parts of the perianth;* some dealt with *the apparent fusion of parts,* and some concerned *the symmetry of the flower.*

The differentiation of a perianth has clearly taken place in some flowers through the transformation of sporophylls, which became sterile and assumed perianth characters (generally those of petals). Such transformations are admirably shown in the passage of stamens into the parts of the perianth in the white water lily, and in the doubling of flowers, where stamens and frequently carpels become petals. It is possible, however, that parts of a perianth may be derived in a reverse direction,— that is, from leaves or bracts on the stem just below the sporophylls. That ordinary leaves can become highly modified and colored to serve the purpose of a perianth is illustrated by the showy bracts of the painted cup, or the flowering dogwood and other species of *Cornus* (Frontispiece). The parts of the simplest types of perianth were probably all similar and largely protective, especially to the flower bud. These later became differentiated into the two sets, sepals and petals, — the latter, and frequently also the former, showy and clearly related to pollination by insects or birds (Chapter XXXII).

The arrangements of the sporophylls and parts of the perianth are, as a rule, spiral in simpler types of flowers, but generally in circles or whorls in higher types. In passing from the spiral to the cyclic arrangements the variable and indefinite numbers of parts tend to become constant. Thus three and multiples of three are the prevailing numbers in the flowers of monocotyledons, while four and five are common numbers in the dicotyledons. A settling of the parts into fixed numbers would be always an important forward step in floral evolution, according to Engler, whether it concerns the perianth, the sporophylls, or both together; for it tends to give definite form to the flower, and thus leads toward the higher conditions. Sometimes a flower will be mixed in the arrangement of its parts, the perianth being cyclic and the stamens and carpels spiral, as in certain buttercups. The establishment of fixed numbers is frequently accompanied by the suppression of some parts (sepals, petals, stamens, or carpels), so that the numbers are variable in different circles.

The apparent fusion of parts, frequently called coalescence, results from the formation of tubular or cup-like outgrowths from zones of tissue below the floral parts, so that they seem to be united. The most complex conditions of flower structure, called *epigyny* (Fig. 136, *C*) and *perigyny* (Fig. 136, *B*), are due to these zonal growths (see Secs. 152, 157, 364). The contrast to epigyny and perigyny is *hypogyny* (Fig. 136, *A*). When petals or sepals are borne on zonal outgrowths the conditions are called, respectively, *sympetaly* and *synsepaly* (Sec. 152). The compound pistil, — that is, a pistil involving two or more carpels, — is one of the highest expressions of zonal growth and is called *syncárpy* (meaning united fruits).

The symmetry of the flower may be either *radial* or *bilateral*, that is with a right and a left half (Sec. 150). Primitive flowers were radially symmetrical, as would be expected from an indefinite number of parts spirally arranged. Bilateral symmetry appears, however, in very many groups and always represents a high degree of floral evolution. It is found more commonly in epigynous and perigynous flowers than in hypogynous, but there is no rule about its relations to these conditions. Bilateral symmetry is usually directly related to methods of flower pollination by insects, for the forms of such flowers are especially adapted to the habits of bees, which light on some expanded lip-like region of the perianth and rummage around, gathering pollen and nectar, and incidentally effecting the pollination of the stigma (Sec. 401).

Bilateral symmetry is generally accompanied by dorsiventrality, which means that the flower hangs in such a position that there is an upper and a lower portion as well as a right and a left half. Excellent illustrations are such lipped flowers as the snapdragons, the mints, and many orchids. An epigynous flower whose symmetry is bilateral and dorsiventral and whose parts, through suppression or other developments, show irregularities which have a clear relation to insect visitations,—these characters give the highest types of flower evolution.

According to Engler, the chief steps in the evolution of the flower may be:

1. The differentiation of a perianth.
2. The change from spiral arrangement of parts, with indefinite numbers, to cyclic arrangements, with fixed numbers.
3. The grouping of parts through zonal growths (coalescence), resulting in syncarpy, perigyny, and epigyny.
4. The change from radial to bilateral symmetry, accompanied by dorsiventrality.
5. To these stages in floral evolution should be added the complexity attained by the massing of numerous flowers in groups or heads (Sec. 165), as in the composite family (daisies, sunflowers, etc.). In the highest expressions of this development the flowers are differentiated so that the outermost of the groups become sterile, but by a remarkable lengthening of their corollas into rays the flower cluster becomes very conspicuous.

All flowers do not, by any means, follow the order of evolution as outlined above, and there are very many special irregularities in different groups. Thus certain flowers of the legume family are bilaterally symmetrical and dorsiventral, but there is no perigyny or epigyny. It is important to note that the higher levels of flower evolution have been developed again and again in unrelated groups of angiosperms independently one of another (as, for example, among the orchids, the legumes, the snapdragons, the mints, etc.). While there is generally an upward evolution of flowers, especially when insect-pollinated, there are in some groups numerous illustrations of floral degeneration.

THE CLASSIFICATION OF THE ANGIOSPERMS

369. The classification of the angiosperms.[1] The subdivision *Angiospermæ* contains two classes:

- Class I. The monocotyledons, or *Monocotyledoneæ*, with an embryo having a single lateral cotyledon.
- Class II. The dicotyledons, or *Dicotyledoneæ*, with an embryo having two terminal cotyledons (including a few exceptions).
  - Sub-Class 1. The *Archichlamydeæ* (meaning primitive floral envelopes), in which the perianth is wanting, or, if present, has its parts entirely separate from one another.
  - Sub-Class 2. The *Metachlamydeæ* (meaning later floral envelopes), or *Sympetalæ*, in which the petals are united or borne on tubular, cup-like, or other forms of zonal outgrowths from the receptacle (Sec. 152).

370. The monocotyledons. Besides having the single cotyledon in the embryo, this group is distinguished from the dicotyledons by having a stem structure, with scattered fibro-vascular bundles, instead of a cyclic arrangement. Consequently there can be no development of a central shaft of wood surrounded by a cylinder of bast, with a cambium tissue lying between the two, as is commonly found in the larger dicotyledons. The leaves are generally *closed* (parallel) veined instead of *open* (netted) veined, and rarely notched, which means that their fibro-vascular bundles come together at the tip or along the edge of the leaf, instead of ending freely as they do in the dicotyledons. The parts of the flower are generally in three or multiples of three.

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[1] The most generally accepted classification of the angiosperms is that of Engler, presented in the *Syllabus der Pflanzenfamilien*, 1903. A brief statement of the chief features of this system will be found in Coulter and Chamberlain, *Morphology of Angiosperms*, 1903.

There are more than 20,000 species of monocotyledons, which are arranged by Engler into 11 orders, the chief of which are:

1. The grass and sedge order, *Graminales,* including more than 6000 species, one of the most successful assemblages of angiosperms and by far the largest in the number of individuals.
2. The palm order, *Palmales,* a very characteristic tropical and sub-tropical group.
3. The lily order, *Liliales,* a large group of almost 5000 species, remarkable for the showiness and symmetry of its flowers.
4. The orchid order, *Orchidales,* containing the large orchid family with more than 5000 species, the largest family in the *Monocotyledoneæ,* and one of the most remarkable groups of seed plants for the beauty and complexity of its flowers and for its peculiar life habits.

371. The dicotyledons. Besides having two cotyledons in the embryo, this group is distinguished from the monocotyledons by having its fibro-vascular bundles formed in a circle. This arrangement makes possible the development of a central shaft of wood (xylem), since the cambium regions of the bundles unite into a cylinder which adds successive layers of wood if the plant is perennial. The bundles in the leaves are strongly developed, much branched, and end freely, so that the leaves are conspicuously open (netted) veined, generally notched, and frequently deeply divided, or compound. The parts of the flowers are mostly in fours and fives in the higher types, except that the number of carpels is commonly less.

There are more than 100,000 species of dicotyledons, and these are arranged by Engler into 34 orders (26 in the *Archichlamydeæ,* and 8 in the *Metachlamydeæ*).

372. The Archichlamydeæ. This sub-class is an immense assemblage, very diverse in character, whose flowers range from primitive types, with indefinite numbers of parts in spiral arrangements, to cyclic flowers with definite numbers, perigyny, epigyny, and syncarpy. Some of the chief orders are:

1. The tree orders, including the willows and poplars (*Salicales*); the walnuts and hickories (*Juglandales*); the birches, alders, beech, chestnut, and oaks (*Fagales*); the elms, figs, mulberries, etc. (*Urticales*).

2. The buttercup order, *Ranunculales,* a large assemblage of about 4000 species, full of interesting gradations in floral evolution, the buttercup family (*Ranunculaceæ*) being an especially good group for such studies.

3. The poppy order, *Papaverales,* comprising the poppies and the large mustard family.

4. The rose order, *Rosales,* an immense group of over 14,000 species, with several large families, such as the legume or pea family, the rose family, etc. The flowers present a greater range of structure than in the buttercup order. Some large groups in the legume family have flowers with well-developed bilateral symmetry and dorsiventrality.

5. The geranium order, *Geraniales,* containing the geraniums, flax, Euphorbias, etc.

6. The violet order, *Violales,* comprising a large number of families and more than 4000 species.

7. The cactus order, *Cactales,* a very remarkable American group of more than 900 species, mostly adapted to desert conditions.

8. The umbel order, *Umbellales,* containing more than 2500 species, mostly in the umbel (parsley) and dogwood families, — the highest order in the series of the *Archichlamydeæ* on account of its epigynous flowers, the reduced number of carpels, and the massing of the flowers in the characteristic umbel, or in close heads surrounded by a corolla-like involucre of bracts, as in the dogwoods (*Cornaceæ,* see Frontispiece).

373. The Metachlamydeæ. The general flower characters of this sub-class are cyclic arrangements of parts with definite numbers, perigyny or epigyny, and a reduced number of carpels in the compound pistil (syncarpy). The corollas are usually showy, the petals being borne on tubular or cup-like outgrowths (sympetaly). The stamens are usually also borne on the same outgrowth with the petals, so that they appear to arise from them (*epipetaly*). The chief orders are:

1. The ericad order, *Ericales*, containing the heath family, a very characteristic group in the northerly parts of America, Europe, and Asia, especially in the mountains.

2. The gentian order, *Gentianales*, with more than 4000 species, including the gentians, olive family, milkweeds, etc.

3. The phlox order, *Polemoniales*, with more than 14,500 species, containing a number of prominent families, as the phloxes, borrages, nightshades, figworts, mints, verbenas, and others. The two-lipped flowers of the mints, figworts, etc., distinguish these families among the *Metachlamydeæ* as the legumes are distinguished among the *Archichlamydeæ*, and the orchids among the monocotyledons.

4. The madder order, *Rubiales*, including the large madder family, the honeysuckles, the valerian family, and the teasels.

5. The bellwort order, *Campanulales*, containing the highest of all angiosperm families, the *Compositæ*, the largest in the number of species (more than 12,000), and one of the most successful groups of plants.

SUMMARY OF THE SPERMATOPHYTES AND THEIR ADVANCES OVER THE PTERIDOPHYTES

374. Summary of the spermatophytes. The chief characters of the spermatophytes and their advances over the pteridophytes are:

1. The retention of the megaspore as an intimate part of the megasporangium (nucellus) to become the embryo sac, and the development of the female gametophyte parasitically within this structure. The degeneration of the female gametophyte in the angiosperms to a group of nuclei within the embryo sac.

2. The origin of the ovule as a new structure from the megasporangium (nucellus), together with enveloping integuments.

3. The development of the pollen tube from the microspore (pollen grain) as a result of the habit of pollination, by which microspores enter the micropyles of the ovules in gymnosperms, and fall upon a receptive structure, the stigma, in angiosperms.

4. The degeneration of the male gametophyte until it is hardly more than a group of nuclei, with accompanying protoplasm, in the pollen grain and its tube. The degeneration of the motile sperms until they are represented by two sperm nuclei alone (cycads and *Ginkgo* excepted, Sec. 348), which are carried by the pollen tube into the embryo sac.

5. The development and retention of the embryo sporophyte within the embryo sac, and the ripening of the ovule into the seed.

6. The massing of the sporophylls on the shoot, accompanied by envelopes which constitute the perianth of the flower. The development in the angiosperms of the megasporophyll, or carpel, into the simple pistil, and the grouping of carpels through zonal growth (syncarpy) to form the compound pistil, so that the ovules become inclosed in an ovule case (ovary). The differentiation of a receptive surface, the stigma, on the pistil upon which the pollen grain may germinate.

7. The differentiation of the parts of the perianth into sepals and petals, and their grouping through zonal growth, together with the stamens, to give perigyny, epigyny, sympetaly, synsepaly, and epipetaly. The development of bilateral symmetry and dorsiventrality.

8. A general development of the sporophytes in many particulars, giving them much greater complexities of tissue structure, growth, and form than those of the pteridophytes.

CHAPTER XXIX

THE EVOLUTION OF THE SPOROPHYTE AND DEGENERATION OF THE GAMETOPHYTE

375. The evolution of the sporophyte. Alternation of generations had its beginnings among the thallophytes, and is clearly shown in the life histories of the red algæ and the sac fungi, but is not so conspicuous there as in the higher divisions of the plant kingdom. Furthermore, the sporophyte generations of these thallophytes do not seem to be related to the sporophytes of the liverworts and the groups above them, but are probably of independent origin.

Consequently the line of evolution, with the remarkable development of the sporophyte and degeneration of the gametophyte, as illustrated by the pteridophytes and spermatophytes, really had its beginning in the lower bryophytes and in the algal ancestry, probably *Chlorophyceæ*, from which they were derived. This algal ancestry, however, is not known, for there are no living algæ that have the combination of characters which would be expected of the ancestors of the bryophytes, — namely, the multicellular sexual organs, together with clearly established sporophyte and gametophyte phases in the life histories.

The bryophytes were responsible for the first great steps in the evolution of the sporophyte toward the conditions presented in the ferns and seed plants. All of the sporophytes of the liverworts and mosses are to a great extent parasitic upon the gametophytes; that is, they take water from them, and probably certain foods in solution. Two important advances appeared in the bryophytes.

First. The spore-forming tissue gradually came to occupy a relatively smaller part of the sporophyte (compare the sporophytes of the *Riccia* group with those of *Marchantia*, *Porella*, and *Anthoceros*). Thus tissue which originally developed spores, or had spore-forming possibilities, became set apart for vegetative functions alone. In this manner the foot and stalk became established in *Marchantia* and *Porella*, and the heavy walls of the spore case in *Anthoceros*. This principle has been called the "sterilization of potential sporogenous tissue," but a simpler expression would be "the assumption of vegetative functions by tissues with spore-forming possibilities."

Second. Portions of the chlorophyll-bearing regions of the sporophytes developed stomata in *Anthoceros* and in some of the mosses, and this was the beginning of the elaborate mechanism for chlorophyll work (photosynthesis), which is developed to such a high degree in the leaves of ferns and seed plants.

The pteridophytes carried the advance much farther, through the third, fourth, fifth, and sixth great steps in the development of the sporophyte.

Third. The sporophyte became independent of the gametophyte by developing roots, and to these added stems and fronds.

Fourth. This condition was associated with the differentiation of a vascular tissue that made it possible for the sporophyte to grow to a considerable height above the ground, (1) by enabling it to maintain a connection with a water supply through the roots, and (2) by providing it with a strong framework throughout the stem and leaves. In their strengthening functions the fibro-vascular bundles were greatly assisted by the development of rigid tissues (schlerenchyma). In other respects, also, the entire tissue structure, or histology, of the sporophyte became much more complicated.

Fifth. Fronds were differentiated into spore leaves, or sporophylls, and vegetative, or foliage leaves. The spore leaves became grouped into cones, and by heterospory were differentiated into microsporophylls and megasporophylls.

Sixth. The embryo sporophyte of heterosporous pteridophytes, through the shortening of the gametophytic phases, came to use and depend upon food stored in the megaspores by the previous sporophyte generation.

The spermatophytes added the final stages in the evolution of the sporophyte, as follows:

Seventh. The ovule arose through the retention of the megaspore (embryo sac) in the megasporangium (nucellus) inclosed by integuments. The development of the embryo sporophyte within the embryo sac, and the ripening of the ovule, produced the seed.

Eighth. The ovule case, or ovary, appeared with the development from one or more megasporophylls, or carpels (frequently with adjacent tissue), of an inclosing structure, the pistil, upon which was differentiated a special region, the stigma, for the reception of the pollen.

Ninth. The stamen was developed from the microsporophyll.

Tenth. Complicated flowers arose by various groupings of the carpels and stamens, together with showy or protective envelopes constituting the perianth.

Eleventh. The flower cluster, or inflorescence, appeared, culminating in the composite head.

Twelfth. The tissues of the spermatophytes became more complicated in many respects than those of the pteridophytes.

376. The degeneration of the gametophyte. Many steps in the degeneration of the gametophyte were closely related to the advances of the sporophyte.

In most of the bryophytes the gametophytes appear as organisms equally complex with the sporophytes, and in many forms they are more complex. Thus the gametophytes of the mosses and leafy liverworts show a considerable advance over the thalloid gametophytes of the simple bryophytes. The thalloid gametophyte, however, seems to have been the type that was passed over to the pteridophytes, and *Anthoceros* probably gives a fair idea of the relative complexity of the two generations at the time when the first pteridophytes arose.

The beginnings of the degeneration of the gametophyte became clearly evident in the pteridophytes when the relatively small and simple prothallium took the place of the large gametophytes, as illustrated in the *Riccia* and *Marchantia* groups. Its further simplification was greatly accelerated by heterospory, passing through four prominent stages:

First. Dependence upon food stored in the microspore and megaspore, together with gradual loss of chlorophyll, reduced the gametophytes to small structures producing relatively few sexual organs and gametes. Thus the gametophytes in the pteridophytes became dependent upon food supplied by the sporophytes by way of the spores, — a relation exactly the reverse of that in the bryophytes.

Second. The gametophytes became differentiated as male and female in sex, associated with the microspores and megaspores, respectively.

The spermatophytes, by means of the seed habit, brought about the greatest changes in the gametophytes, as follows:

Third. The female gametophyte degenerated to such an extent by the retention of the megaspore (embryo sac) in the megasporangium (nucellus) that the archegonium lost its form and finally became represented in its essentials by the egg alone. The vegetative tissue became reduced until only a few nuclei of uncertain rélationship (antipodal and polar nuclei) remain.

Fourth. The male gametophyte degenerated in structure in a similar manner until the antheridium disappeared, and the numerous ciliated sperms of the pteridophytes were represented by only two sperm nuclei, with associated protoplasm. Vegetative tissue was reduced until only a single nucleus remained in the angiosperms to represent sterile cells of a male gametophyte.

There arose, however, by means of the seed habit an activity on the part of the male gametophyte which is one of the most remarkable developments in plant evolution. The appearance of the pollen tube, with its parasitic relations to the sporophyte, is a very complex life relation. This was the chief cause of floral evolution, with all its wonderful diversities of form and structure in relation to insect life, — diversities assumed to carry out the relation of flowers to insect carriers of pollen.

Part II of this work has given an outline of the evolution and classification of plants based on comparative studies of their morphology. The conclusions are necessarily speculative and philosophical, for we have no means of knowing exactly what has happened throughout the geological ages. The fossil remains of plants are very helpful in certain groups, as the pteridophytes and spermatophytes, but they are fragmentary and relatively few, except for such periods as those when coal or coal-like deposits were formed. Consequently our conclusions as to the evolutionary history of plants must be founded chiefly on studies of life histories and the comparative morphology of living groups. In spite of difficulties, the plant morphologist has been able to establish a classification of plants, based on kinship, so as to determine the framework of evolutionary lines with remarkable clearness, and these conclusions give to botany its chief interest on the side of morphology. It is not strange that the development of exact ideas in regard to plant evolution should have lagged behind the progress made in that line in animal evolution, since the paleontological evidence available for the botanist, as above stated, is so scanty. It is only within a very few years that any attempt has been made to introduce beginners in botany to the evolutionary history of plants, and popular knowledge of the subject is now no farther advanced than was knowledge of animal evolution more than thirty years ago.

PART III

ECOLOGY AND ECONOMIC BOTANY

CHAPTER XXX

PARASITES AND CARNIVOROUS PLANTS

377. Ecology.* *Plant ecology* discusses the way in which plants get on with their animal and plant neighbors and, above all, the way in which they adjust themselves to the nature of the soil and climate in which they live. Ecology, in short, treats of the relations of plants to the world about them. A good deal of what has been said in previous chapters on such topics as parasitic plants, climbing plants, the movements of leaves, the coating of hairs on stems and leaves, the storage of water in epidermis cells, is really ecological botany, although it is not so designated in the sections where it occurs. It is evident enough that much of the subject-matter of ecology is merely a special department of physiology, but another portion of it forms an important part of plant geography.

378. Parasites. By the term *parasite* in botany, a plant is meant which draws its food supply wholly or partially from another living plant or animal called the *host*. In Sec. 29 the life history of a familiar parasite, the dodder, was briefly sketched, and the parasitic fungi among spore plants have been discussed in Chapter XXII.

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* TO THE INSTRUCTOR: The treatment of the subject of ecology will pertain almost entirely to seed plants. Many ecological topics relating to spore plants have been discussed under the various groups described in Part II.

379. Half-parasitic seed plants. Half parasites, or partial parasites, are those which take a portion of their food, or of raw materials to make food, from their host and manufacture the rest for themselves. Usually they take mainly the newly absorbed soil water from the host and do their own starch making by combining the carbon dioxide, which they absorb through their leaves, with the water stolen by the parasitic roots, or *haustoria*, imbedded in the wood of the host. Evidently the needed water may just as well be taken from the underground parts of the host as from the upper portions, and accordingly many half parasites are parasitic on roots. This is the case with many of the beautiful false foxgloves (*Gerardia*), with the painted cup (*Castillea*), and some species of false toadflax (*Comandra*) and some orchids.[1] Usually these root parasites are not recognized by non-botanical people as parasites at all, but in Germany a species common in grain fields[2] and the eyebright, which abounds in grass fields, are respectively known as "hunger" and "milk thief," from the injury they do to the plants on which they fasten themselves. The mistletoe is a familiar example of a half parasite which roots on branches. Among the scanty belts of cottonwood trees along streams in New Mexico it is necessary to lop off the mistletoe every year to give the tree any chance to grow. Half parasites may be known from plants that are fully parasitic by having green or greenish foliage, while complete parasites have no chlorophyll and so are not at all green.

380. Wholly parasitic seed plants. These are so nearly destitute of the power of photosynthesis that they must rob other plants of all needed food or die of starvation. Some, like the cancer root (*Aphyllon*) are root parasites; others, like the dodder (Fig. 16), are parasitic on stems above ground. The most dependent species of all, such as the flax dodder, can live on only one kind of host, while the coarse orange-stemmed

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[1] See Bergen, *Flora of the Northeastern States.*

[2] *Alectorolophus hirsutus.*

dodder,[1] which is common all over the central and the north-eastern states, grows freely on many kinds of plants, from golden-rods to willows.

381. Saprophytes. A *saprophyte* (meaning decay plant) is a plant of which the nutrition is largely or wholly dependent on the absorption of organic material, usually when in a state of fermentation or decay. Most plants of this kind are fungi (Chapter XXII), but there are a few saprophytic seed plants, the Indian pipe, so common in coniferous woods, being one of the most familiar. In appearance the saprophytes resemble parasites so far as the absence of green color is concerned and of course they do little or no photosynthetic work.

FIG. 311. Common pitcher plant (*Sarracenia purpurea*)

At the right, one of the pitcher-like leaves is shown in cross section

382. Carnivorous plants. In the ordinary pitcher plants (Fig. 311) the leaf appears in the shape of a more or less hooded pitcher. These pitchers are usually partly filled with water, and in this water very many drowned and decaying insects are commonly to be found. The insects have flown or crawled into the pitcher, and, once inside, have been unable to escape on account of the dense growth of bristly hairs about the mouth, all pointing inward and downward. How much the

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[1] *Cuscuta Gronovii.*

FIG. 312. Sundew (*Drosera rotundifolia*)

common American pitcher plants depend for nourishment on the drowned insects in the pitchers is not definitely known, but it is certain that some of the tropical species require such food.[1]

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[1] Where the *Sarracenia* is abundant it will be found interesting and profitable to make a careful class study of its leaves. See Geddes, *Chapters in Modern Botany*, Chapters I and II.

In other rather common plants, the sundews, insects are caught by a sticky secretion which proceeds from hairs on the leaves. In one of the commonest sundews (Fig. 312) the leaves consist of a roundish blade, borne on a moderately long petiole. On the inner surface and round the margin of the blade are borne a considerable number of short bristles, each terminating in a knob, which is covered with a clear, sticky liquid. When a small insect touches one of the sticky knobs it is held fast, and the hairs at once begin to close over it, as shown in Fig. 313. Here it soon dies and then usually remains for many days, while the leaf pours out a juice by which the soluble parts of the insect are digested. The liquid containing the digested portions is then absorbed by the leaf and contributes an important part of the nourishment of the plant, while the undigested fragments, such as legs, wing cases, and so on, remain on the surface of the leaf or may drop off after the hairs let go their hold on the captive insect.

FIG. 313. Leaves of sundew

The one at the left has all its tentacles closed over captured prey; the one at the right has only half of them thus closed. Somewhat magnified. — After Darwin

In the Venus flytrap, which grows in the sandy regions of eastern North Carolina, the mechanism for catching insects is still more remarkable. The leaves, as shown in Fig. 314, terminate in a hinged portion, which is surrounded by a fringe of stiff bristles. On the inside of each half of the trap grow three short hairs. The trap is so sensitive that when these hairs are touched it closes with a jerk and very generally succeeds in capturing the fly or other insect which has sprung it. The imprisoned insect then dies and is digested, somewhat as in the case of those caught by the sundew, after which the trap reopens and is ready for fresh captures.

383. Object of catching animal food. It is easy to understand why a good many kinds of plants have taken to catching insects and absorbing the digested products. Carnivorous, or flesh-eating, plants belong usually to one of two classes as regards their place of growth; they are bog plants or air plants. In either case their roots find it difficult to secure much nitrogen-containing food,—that is, much food out of which proteid material can be built up. Animal food, being itself largely proteid, is admirably adapted to nourish the growing parts of plants, and those which could develop insect-catching powers would stand a far better chance to exist as air plants or in the thin, watery soil of bogs than plants which had acquired no such resources.

FIG. 314. Venus flytrap (*Dionœa muscipula*)

CHAPTER XXXI

HOW PLANTS PROTECT THEMSELVES FROM ANIMALS

384. Destruction by animals. All animals are supported directly or indirectly by plants. In some cases the animal secures its food without much damage to the plant on which it feeds. Browsing on the lower branches of a tree may do it little injury, and grazing animals, if not numerous, may not seriously harm the pasture in which they feed. Fruit-eating animals may even be of much service by dispersing seeds (Sec. 420). But seed-eating birds and quadrupeds, animals which (like the hog) dig up fleshy roots, rootstocks, tubers, or bulbs, and eat them, or animals which (like the sheep) graze so closely as to expose the roots of grasses or even of forest trees to be parched by the sun, destroy immense numbers of plants. Many trees, as the apple, peach, and black locust, have the trunk fatally weakened by the boring larvæ of insects. Leaf-eating insects, such as grasshoppers and caterpillars, cause immense damage to foliage, and others, like the chinch bug so destructive to grain crops, suck the juices from roots, stems, or leaves.

385. Some modes of protection from animals. Many of the characteristics of plants may be wholly or partly due to adaptations for protective purposes, while in particular cases we cannot be sure of the fact. Perching on lofty rocks or on branches of trees, burying the perennial part (bulb, rootstock, etc.) underground, growing in dense masses, like a canebrake or a thicket of blackberry bushes, — all such habits of plants may be partly or altogether valuable to the plant as means of avoiding the attacks of animals, but this cannot be proved. On the other hand, there are plenty of instances of structures, habits, or accumulations of stored material in their tissue which plants seem to have acquired mainly or entirely as means of defense. Some of the most important are:

1. The habit of keeping a bodyguard of ants.
2. Forming tough, corky, woody, limy, or flinty, and therefore nearly uneatable, tissue.
3. Arming exposed parts with cutting edges, sharp or stinging hairs, prickles, or thorns.
4. Accumulating unpleasant or poisonous substances in exposed parts.

386. Ant plants. Some ants live on vegetable food, but most of them eat only animal food, and these latter are extremely voracious. It has been estimated by a careful scientist, an authority on this subject, that the ants of a single nest sometimes destroy as many as one hundred thousand insects in a day. The Chinese orange growers in the province of Canton have found how useful ants may be as destroyers of other insects, and so they place ant nests in the orange trees and extend bamboos across from one tree to another, to serve as bridges for the ants to travel on.

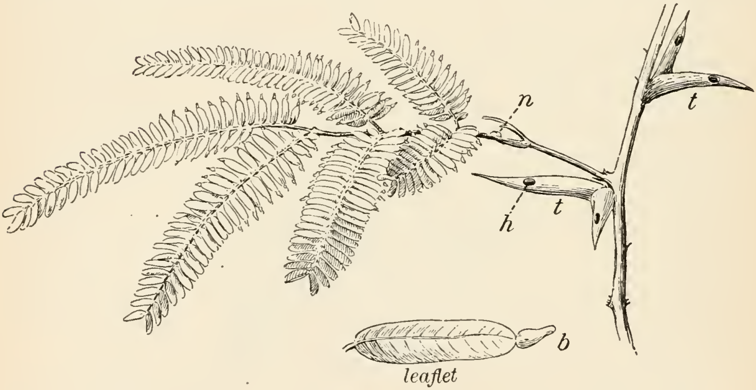

Fig. 315. An ant plant (*Acacia sphærocephala*)

t, thorns; *h*, hole in thorn; *n*, nectary; *b*, Belt's body on tip of leaflet. — After Schimper

Certain tropical trees offer ants special inducements to establish colonies on their trunks and branches. The attractions which are offered to ants by various kinds of trees differ greatly. One of the most interesting adaptations is that of an acacia (Fig. 315), which furnishes little growths at the ends of the leaflets which serve as ant food. These little growths are known from their discoverer as Belt's bodies. The ants bore holes into the large, hollow, stipular thorns shown in the figure, live in these thorns, feed on the Belt's bodies, and protect the acacia from insect and other enemies. A nectary on the leaf furnishes additional food to the ant inhabitants of the tree. A great multitude of plants, some of them herbs, offer more or less important inducements to attract ant visitors; the species which are known to do this number over three thousand.[1]

387. Plants of uneatable texture. Whenever tender and juicy herbage is to be had, plants of hard and stringy texture are left untouched by grazing animals. The flinty-stemmed horsetails (*Equisetum*, Sec. 316) and the dry, tough rushes are familiar examples of uneatable plants of damp soil. In pastures there grow such perennials as the bracken fern and the hardhack of New England and the ironweed and vervains of the central states, which are so harsh and woody that the hungriest browsing animal is rarely, if ever, seen to molest them. Still other plants, like the knotgrass and cinquefoil of our dooryards, are doubly safe, from their growing so close to the ground as to be hard to graze, and from their woody and unpalatable nature. The date palm, which can easily be raised from the seed in the botanical laboratory, is an excellent instance of the same uneatable quality, found in a tropical or sub-tropical plant. Other good examples are the shrubs of heath lands and of such coriaceous, or leathery-leafed, thickets as the Australian scrub and the California chaparral.

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[1] Possibly in many cases the attractiveness of plants for ants is only incidental and has not been evolved with direct reference to the protection to be rendered by these insects.

388. Plants with weapons for defense.[1] Multitudes of plants, which might otherwise have been subject to the attacks of grazing or browsing animals, have acquired what have with reason been called weapons. Shrubs and trees not infrequently produce sharp-pointed branches, familiar in our own crab apple, wild plum, thorn trees, and, above all, in the honey locust (Fig. 35), whose formidable thorns often branch in a very complicated manner. It is noteworthy that the protection given by thorns is not from those of the season, but from the dry and hard ones of preceding years.

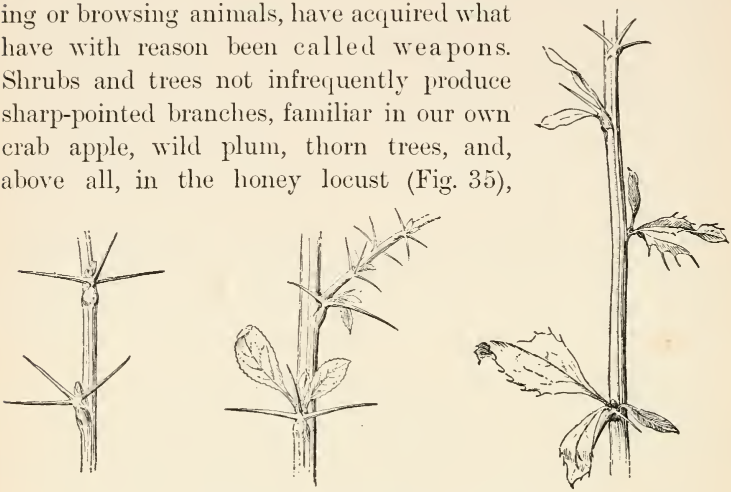

FIG. 316. Spiny leaves of barberry

FIG. 317. Spiny leaf of a nightshade (*Solanum atropurpureum*)

Leaves modified into thorns are very perfectly exemplified in the barberry (Fig. 316). It is much commoner, however, to find the leaf extending its midrib or its veins out into spiny points, as the thistle does, or bearing spines or prickles on its midrib, as is the case with some nightshades (Fig. 317) and with so many roses.

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[1] See Kerner and Oliver, *Natural History of Plants*, Vol. I, p. 430.

Prickles, which are merely hard, sharp-pointed projections from the epidermis, are of too common occurrence to need illustration.

Thorns are often found to be modified stipules, and in our common locust (Fig. 319) the bud, or the very young shoot which proceeds from it, is admirably protected by the jutting thorn of the previous year on either side.

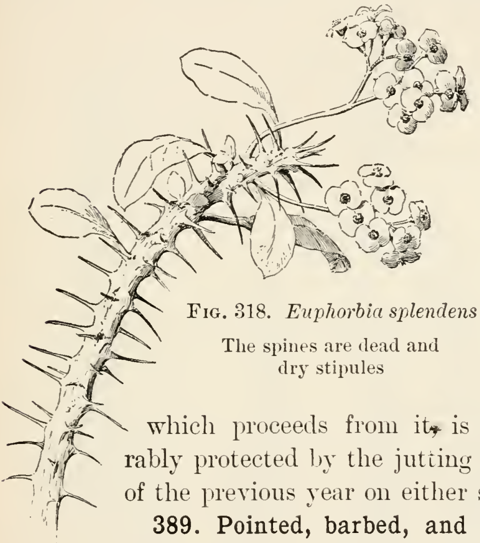

FIG. 318. *Euphorbia splendens*

The spines are dead and dry stipules

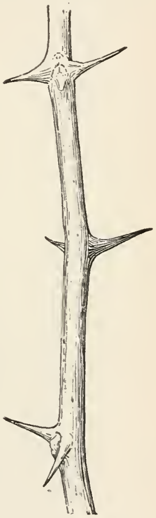

FIG. 319. Thorn stipules of locust

389. Pointed, barbed, and stinging hairs. On many plants needle-pointed hairs form efficient defensive weapons. Sometimes these hairs are roughened, like those of the bugloss (Fig. 320, *b*); sometimes they are decidedly barbed. If the barbs are well developed, as they are in the small but formidable bristles of prickly pear cactuses, they may cause the hairs to travel far into the flesh of animals and cause intense pain. In the nettle (Fig. 320, *a*) the hairs are efficient stings, with a brittle tip, which on breaking off exposes a sharp, jagged tube full of irritating fluid. These tubular hairs, with their poisonous contents, will be found sticking in the skin of the hand or the face after incautious contact with nettles, and the violent itching which follows is only too familiar to most people.

390. Cutting leaves. Some grasses and sedges are generally avoided by cattle because of the sharp, cutting edges of their leaves, which will readily slit the skin of one's hand if they are drawn rapidly through the fingers. Under the microscope the margins of such leaves are seen to be regularly and thickly set with sharp teeth like those of a saw (Fig. 320, *c*, *d*).

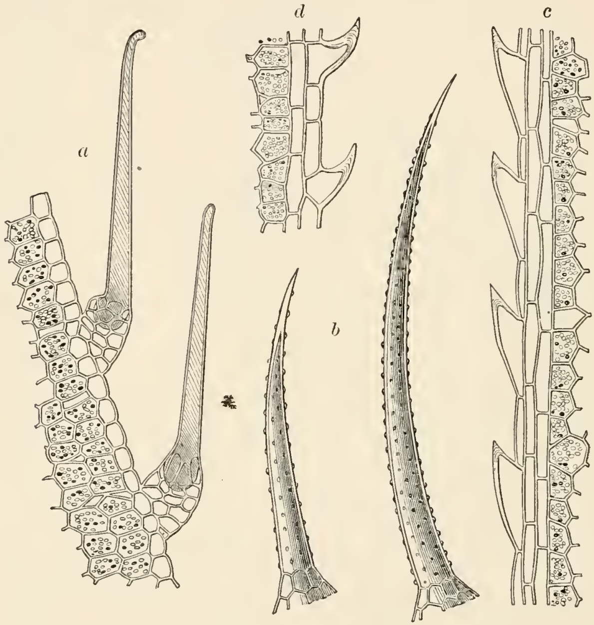

FIG. 320. Stinging hairs and cutting leaves

a, stinging hairs on leaf of nettle; *b*, bristle of the bugloss; *c*, barbed margin of a leaf of sedge; *d*, barbed margin of a leaf of grass. All much magnified.—After Kerner

391. Weapons of desert plants. In temperate regions, where vegetation is usually abundant, such moderate means of protection as have just been described are generally sufficient to insure the safety of the plants which have developed them. But in desert or semi-desert regions the extreme scarcity of plant life especially exposes the few plants that occur there to the attacks of herbivorous animals. Accordingly, great numbers of desert plants are characterized by nauseating or poisonous qualities or by the presence of astonishingly developed thorns (Figs. 50, 357), while some combine both of these means of defense.

392. Offensive or poisonous plants. A disgusting smell is one of the common safeguards which keep plants from being eaten. The dog fennel (Fig. 364), the hound's tongue (*Cynoglossum*), the Martynia, and the tomato plant are common examples of rank-smelling plants which are offensive to most grazing animals and so are let alone by them. Oftentimes, as in the case of the jimson weed (*Datura*), the tobacco plant, and the poisonous hemlock (*Conium*), the smell serves as a warning of the poisonous nature of the plant.

A bitter, nauseating, or biting taste protects many plants from destruction by animals. Buckeye, horse-chestnut, and buckthorn twigs and leaves are so bitter that browsing animals and most insects let them alone. Tansy, ragweed, boneset, southernwood, and wormwood are safe for the same reason. The nauseous taste of many kinds of leaves and stems, such as those of the potato, and the fiery taste of peppercorns, red peppers, mustard, and horse-radish, make these substances uneatable for most animals. Probably both the smell and the taste of onions serve to insure the safety of the bulbs from the attacks of most grubs, and the hard corm of the jack-in-the-pulpit (*Arisæma*) is carefully let alone on account of the blistering nature of its contents.

Poisonous plants are usually shunned by grown-up animals unless they are famished, though the young ones will sometimes eat such plants and may be killed by them. Almost any part of a poisonous species may contain the poison characteristic of the plant, but, for obvious reasons, such substances are especially apt to be stored in the parts of the plant where its supply of reserve food is kept.

CHAPTER XXXII

POLLINATION OF FLOWERS AND PROTECTION OF POLLEN

393. Topics of the Chapter. The ecology of flowers is concerned mainly with the means by which the transference of pollen, or *pollination*, is effected, and with the ways in which pollen is kept away from undesirable insect visitors and from rain.

394. Cross pollination and self pollination. It was long supposed by botanists that the pollen of any bisexual flower needed only to be placed on the stigma of the same flower to insure satisfactory fertilization. But in 1857 and 1858 the great English naturalist, Charles Darwin, stated that certain kinds of flowers were entirely dependent for fertilization on the transference of pollen from one plant to another. It was also shown that probably nearly all attractive flowers, even if they can produce some seed when self-pollinated, do far better when pollinated from the flowers of another plant of the same kind.[1] This important fact was established by a long series of experiments on the number and vitality of seeds produced by a flower when treated with its own pollen, or *self-pollinated*, and when treated with pollen from another flower of the same kind, or *cross-pollinated*.[2]

Another important advantage of cross pollination is that it tends to give the offspring additional variability (Chapter XL), and thus enables them better to adapt themselves to changing environment or to any difficult conditions.

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[1] See Darwin, *Cross and Self Fertilization in the Vegetable Kingdom* (especially Chapters I and II).

[2] On dispersion of pollen, see Kerner and Oliver, *Natural History of Plants*, Vol. II, pp. 129–287.

It should always be kept in mind that many of the most successful plants, including a large number of troublesome weeds, are capable of self pollination.

395. Wind-pollinated flowers.[1] It has already been mentioned that some pollen is dry and powdery, and other kinds are more or less sticky. Pollen of the dusty sort is light, and therefore adapted to be blown about by the wind. Any one who has been much in cornfields after the corn has "tasseled" has noticed the pale yellow, dusty pollen which flies about when a cornstalk is jostled, and which collects in considerable quantities on the blades of the leaves. Corn is monœcious, but fertilization is best accomplished by pollen blown from the "tassel" (stamens) of one plant being carried to the "silk" (stigma and style of the pistils) of another plant. This is well shown by the fact, familiar to every observing farmer's boy, that solitary cornstalks, such as often grow very luxuriantly in an unused barnyard or similar locality, bear very imperfect ears or none at all. The common ragweed is remarkable for the great quantities of pollen which shake off on to the shoes or clothes of the passer-by, and it is wind-pollinated. So, too, are the pines, and these produce so much pollen that it has been mistaken for showers of sulphur, falling often at long distances from the forests where it was produced. The pistil of wind-pollinated flowers is often feathery and thus adapted to catch flying pollen grains (Fig. 321). Other characteristics of such flowers are the inconspicuous character of their perianth, which is usually green or greenish, the absence of odor and of nectar, the regularity of the corolla, and the development of the flowers before the leaves or their occurrence on stalks raised above the leaves.

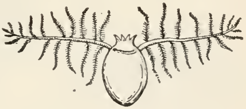

FIG. 321. Pistil of a grass, provided with a feathery stigma, adapted for wind-pollination

After Thomé

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[1] See Miss Newell, *Botany Reader*, Part II, Chapter VII.

Pollen is, in the case of a few aquatic plants, carried from flower to flower by the water in which the plant grows.

396. Insect-pollinated flowers. Most plants which require cross pollination depend upon insects as pollen carriers,[1] and it may be stated as a general fact that the showy colors and markings of flowers and their odors all serve as so many advertisements of the nectar (commonly but wrongly called honey) or of the nourishing pollen which the flower has to offer to insect visitors.

Many insects depend mainly or wholly upon the nectar and the pollen of flowers for their food. Such insects usually visit during any given trip only one kind of flower, and therefore carry but one kind of pollen. Going straight from one flower to another with this, they evidently waste far less pollen than the wind or water must waste. It is therefore clearly advantageous to flowers to develop such adaptations as fit them to attract insect visitors, and to give pollen to the latter and receive it from them.

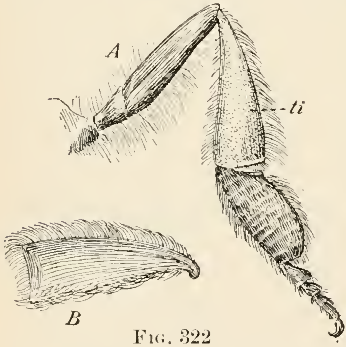

Fig. 322

A, right hind leg of a honeybee (seen from behind and within); *B*, the tibia; *ti*, seen from the outside, showing the collecting basket formed of stiff hairs. — After Müller

397. Pollen-carrying apparatus of insects.[2] Ants and some beetles which visit flowers have smooth bodies, to which little pollen adheres, so that their visits are often of slight value to the flower, but many beetles, all butterflies and moths, and most bees have bodies roughened with scales or hairs, which hold a good deal of pollen entangled. In the common honeybee (and in many other kinds) the greater part of the insect is hairy, and there are special collecting baskets, formed by bristle-like hairs, on the hind legs (Fig. 322).

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[1] A few are pollinated by snails; many more by humming birds and other birds.

[2] See P. Knuth, *Handbuch der Blüthenbiologie*, Vol. I.

It is easy to see the load of pollen accumulated in these baskets after such a bee has visited several flowers. Of course the pollen which the bee packs in the baskets and carries off to the hive, to be stored for food, is of no use in pollination. In fact, such pollen is in one sense entirely wasted. But since such bees as have these collecting baskets are the most industrious visitors to flowers, they accomplish an immense share of the work of pollination by means of the pollen grains, which stick to their hairy coats and are then transferred to other flowers of the same kind next visited by the bee.

398. Nectar and nectaries. Nectar is a sweet liquid which flowers secrete and which attracts insects. After partial digestion in the crop of the bee, nectar becomes honey. Those flowers which secrete nectar usually do so by means of *nectar glands*, small organs situated often near the base of the flower, as shown in Fig. 323. Sometimes the nectar clings in droplets to the surface of the nectar glands; sometimes it is stored in little cavities or pouches called *nectaries*. The pouches at the bases of columbine petals are among the most familiar of nectaries.

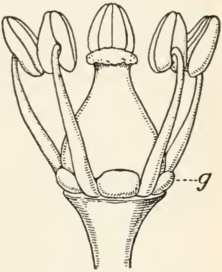

Fig. 323. Stamens and pistil of the grape (magnified), with a nectar gland *g* between the stamens

After Decaisne

399. Odors of flowers. The acuteness of the sense of smell among insects is a familiar fact. Flies buzz about the wire netting which covers a piece of fresh meat or a dish of sirup, and bees, wasps, and hornets will fairly besiege the window screens of a kitchen where preserving is going on. Many plants find it possible to attract as many insect visitors as they need without giving off any scent perceptible to us, but small flowers, like the mignonette, and night-blooming ones, like the white tobacco and the evening primrose, are sweet-scented to attract night-flying moths. It is interesting to observe that the majority of the flowers which bloom at night are white or yellow, and that they are much more generally sweet-scented than flowers which bloom during the day. Many are odorous during only a few hours of the twenty-four, just at the time when the special insects which pollinate them are on the wing. A few flowers (purplish, brownish, or greenish colored) are carrion-scented and attract flies.

400. Colors of flowers. Flowers which are of any other color than green probably in most cases display their colors to attract insects, or occasionally birds. The principal color of the flower is most frequently due to showy petals; sometimes, as in the anemone and marsh marigold, it belongs to the sepals; and not infrequently, as in some cornels (Frontispiece) and Euphorbias (Fig. 318), the involucre is more brilliant and conspicuous than any part of the flower strictly so called. In the willows and chestnuts the stamens are the conspicuous parts.

Different kinds of insects appear to be especially attracted by different colors. In general, dull yellow, brownish, or dark purple flowers, especially if small, seem to depend largely on the visits of flies. Red, violet, and blue are the colors by which bees and butterflies are most readily enticed. The power of bees to distinguish colors has been shown by a most interesting set of experiments in which daubs of honey were put on slips of glass laid on separate pieces of paper, each of a different color, and exposed where bees would find them.[1]

It is certain, however, that colors are less important means of attraction than odors from the fact that insects are extremely near-sighted. Butterflies and moths cannot see distinctly at a distance of more than about five feet, bees and wasps at more than two feet, and flies at more than two and a fourth feet. Probably no insects can make out objects clearly more than six feet away.[2] Yet it is quite possible that their attention is attracted by colors at distances greater than those mentioned.

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[1] See Lubbock, *Flowers, Fruits, and Leaves*, Chapter I. On the general subject of colors and odors in relation to insects, see P. Knuth, *Handbuch der Blüthenbiologie.*

[2] See Packard, *Text-Book of Entomology*, p. 260.

401. Facilities for insect visits. Regular flowers with radial symmetry usually have no special adaptations to make them singly accessible to insects, but lie open to all comers. They do, however, make themselves much more attractive and afford especial inducements in the matter of saving time to flower-frequenting insects by being grouped. This purpose is undoubtedly served by dense flower clusters, such as those of the lilac, the phlox, and the elder, and especially by heads like those of the button bush (*Cephalanthus*) and by the peculiar form of head found in so-called composite flowers, like the sunflower, the bachelor's button, and the yarrow (Fig. 144). In many such clusters the flowers are specialized, some carrying a showy strap-shaped corolla, to serve as an advertisement of the nectar and pollen contained in the inconspicuous tubular flowers. Flowers with bilateral symmetry probably always are more or less adapted to particular insect (or other) visitors. The adaptations are extremely numerous; here only a very few of the simpler ones will be pointed out. Where there is a drooping lower petal or, in the case of a sympetalous corolla, a lower lip, this serves as a perch upon which flying insects may alight and stand while they explore the flower, as the beetle is doing in Fig. 324. In Fig. 325 one bumblebee stands with her legs partially encircling the lower lip of the dead-nettle flower, while another perches on the sort of grating made by the stamens of the horse-chestnut flower. The honeybee entering the violet clings to the beautifully bearded portion of the two lateral petals, while she sucks the nectar from the *spur* beneath. All bilaterally symmetrical flowers seem to be specially adapted to compel visiting insects to enter them in the best way to secure transference of pollen.

Fig. 324. A beetle on the flower of the twayblade

Slightly enlarged.—After Behrens

402. Protection of pollen from unwelcome visitors. It is usually desirable for the flower to prevent the entrance of small creeping insects, such as ants, which carry little pollen and eat a relatively large amount of it. The means adopted to secure this result are many and curious. In some plants, as the common catchfly, there is a sticky ring about the peduncle, some distance below the flowers, and this forms an effectual barrier against ants and like insects. In a few plants, as the teasel and the cup plant (*Silphium perfoliatum*), rain water collects at the junctions of the leaves with the stem and forms an effectual barrier against creeping insects. Very frequently the calyx tube is covered with hairs, which are sometimes sticky. How these thickets of hairs may appear to a small insect can perhaps be realized from Fig. 326.[1]

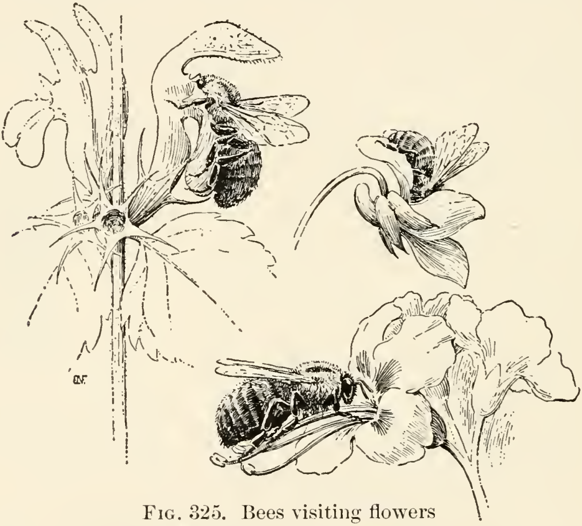

FIG. 325. Bees visiting flowers

At the left, a bumblebee on the flower of the dead nettle; below, a similar bee in the flower of the horse-chestnut; above, a honeybee in the flower of a violet. Modified. — After Behrens

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[1] On protection of pollen, see Kerner and Oliver, *Natural History of Plants*, Vol. II, pp. 95–109.

Sometimes the recurved petals or divisions of the corolla stand in the way of creeping insects. In other cases the throat of the corolla is much narrowed or closed by hairs, or by appendages. Those flowers which have one or more sepals or petals prolonged into spurs, like the nasturtium and the columbine, are inaccessible to most insects except those which have a tongue or a sucking tube long enough to reach to the nectary at the bottom of the spur. The large sphinx moth, shown in Fig. 327, which is a common visitor to the flowers of the

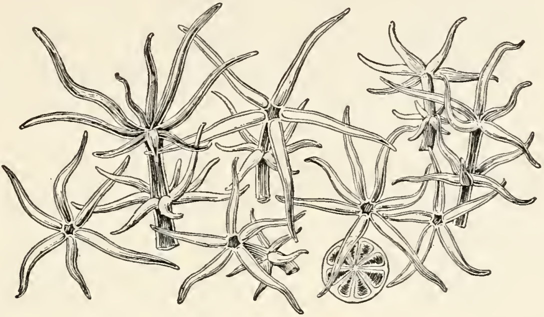

Fig. 326. Branching hairs from the outside of the corolla of the common mullein

Magnified. — After Tschirch

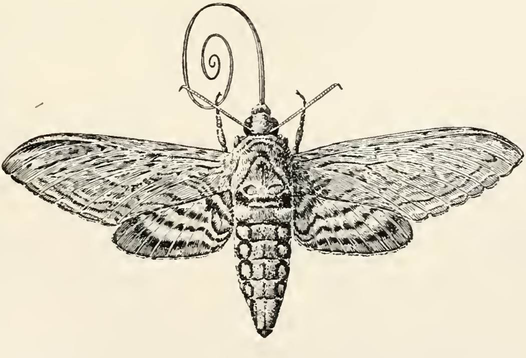

Fig. 327. A sphinx moth, with a long sucking tube

evening primrose, is an example of an insect especially adapted to reach deep into long tubular flowers.

A little search among flowers, such as those of the columbine and the foxglove, will usually disclose many which have had the corolla bitten through by bees which are unable (or unwilling to take the trouble) to get at the nectar by fair means, and which therefore steal it.

403. Bird-pollinated flowers. Some flowers with very long tubular corollas depend entirely upon birds to carry their pollen for them. Among garden flowers the gladiolus, the scarlet salvia, the canna, and the trumpet honeysuckle are largely dependent upon humming birds for their pollination. The wild balsam, or jewelweed, the swamp thistle, and the trumpet creeper are also favorite flowers of the humming bird.

404. Prevention of self pollination. Diœcious flowers are, of course, quite incapable of self pollination. Pistillate monœcious flowers may be pollinated by staminate ones on the same plant, but this does not secure as good seed as is secured by having pollen brought to the pistil from a different plant of the same kind.

In perfect flowers self pollination would commonly occur unless it were prevented by the action of the essential organs or by something in the structure of the flower. In reality, many flowers which at first sight would appear to be designed to secure self pollination are almost or quite incapable of it. Frequently the pollen from another plant of the same species prevails over that which the flower may shed on its own pistil, so that when both kinds are placed on the stigma at the same time it is the foreign pollen which causes fertilization. But apart from this fact there are several means of insuring the presence of foreign pollen, and only that, upon the stigma, just when it is mature enough to receive pollen tubes.

405. Stamens and pistils maturing at different times. If the stamens mature at a different time from the pistils, self pollination is as effectually prevented as though the plant were diœcious. This unequal maturing, or *dichogamy*, occurs in many kinds of flowers. In some, the figwort and the common plantain for example, the pistil develops before the stamens, but usually the reverse is the case. The *Clerodendron*,[1] a tropical African flower (Fig. 328), illustrates in a most striking way the development of stamens before the pistil. The insect visitor, on its way to the nectary, can hardly fail to brush against the protruding stamens of the flower in its earlier stage, *A*, but it cannot deposit any pollen on the stigmas, which are immature, shut together, and tucked aside out of reach. On flying to a flower in the later stage the pollen just acquired will be

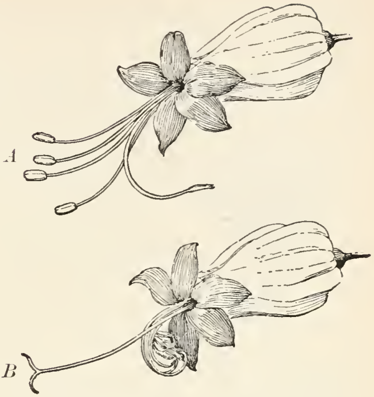

FIG. 328. Flower of *Clerodendron* in two stages

In *A* (earlier stage) the stamens are mature, while the pistil is still undeveloped and bent to one side. In *B* (later stage) the stamens have withered, and the stigmas have separated, ready for the reception of pollen. — After Gray

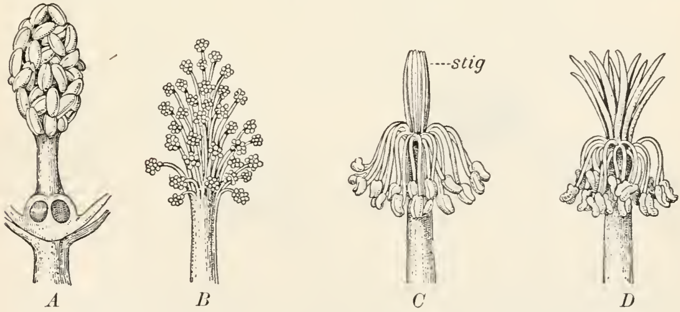

FIG. 329. Provisions for cross pollination in the high mallow

A, essential organs as found in the bud; *B*, same in the staminate stage, the anthers discharging pollen, pistils immature; *C*, intermediate stage (*stig*, the united stigmas); *D*, pistillate stage, the stigmas separated, stamens withered. — After Müller

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[1] *C. Thompsoniæ.*

lodged on the prominent stigmas and thus produce the desired cross pollination.

Closely related flowers often differ in their plan of pollination. The high mallow (a plant cultivated for its purplish flowers), which has run wild to some extent, is admirably adapted to secure cross pollination, since when its stamens are shedding pollen, as in Fig. 329, *B*, the pistils are incapable of receiving it, while when the pistils are mature, as in *D*, the stamens are quite withered. In the common low mallow of our dooryards and waysides insect pollination may occur, but if it does not, the curling stigmas finally come in contact with the projecting stamens and receive pollen from them, as is indicated in Fig. 330.

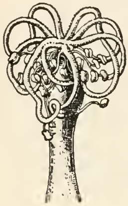

FIG. 330. Stamens and pistils of round-leafed mallow

The stigmas curled round among the stamens to admit of self pollination. — After Müller

406. Movements of floral organs to aid in pollination. Besides the slow movements which the stamens and pistil make in such cases as those of the *Clerodendron* and the mallow, already described, the parts of the flower often admit of considerable and rather quick movements that assist the insect visitor to become dusted or smeared with pollen.

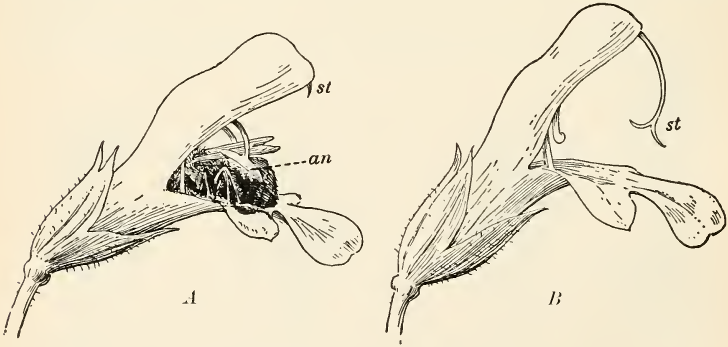

FIG. 331. Two flowers of common sage, one of them visited by a bee

After Lubbock

In some flowers whose stamens perform rapid movements when an insect enters, it is easy to see how directly useful the motion of the stamens is in securing cross pollination. The stamens of the laurel (*Kalmia*) are held in a bent position by the expanded corolla, and when liberated by a touch throw little masses of pollen, with a quick jerk, against the body of the visiting insect. Barberry flowers have filaments which are sensitive on the inner side near the base, and when touched make the anther spring up against the visitor and dust him with pollen. The common garden sage matures its anthers earlier than its stigmas. In Fig. 331, *A*, the young flower is seen, visited by a bee, and one anther, *an*, is shown pressed closely against the side of the bee's abdomen. The stigma, *st*, is hidden within the upper lip of the corolla. In *B*, an older flower, the anthers have withered and the stigma is now lowered so as to brush against the body of any bee which may enter. A little study of Fig. 332 will make clear the way in which the anthers are hinged, so that a bee striking the empty or barren anther lobes, *a*, knocks the pollen-bearing lobes, *a′*, into a horizontal position, so that they will lie closely pressed against both sides of its abdomen. Many stigmas, as those of catalpa and trumpet creeper, close as soon as they are pollinated.

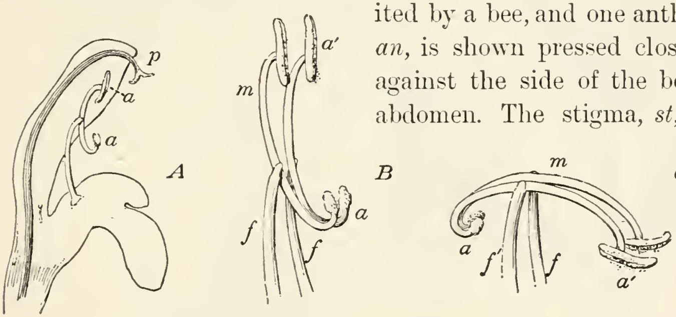

Fig. 332. Flower and stamens of common sage

A, *p*, stigma; *a*, anthers. *B*, the two stamens in ordinary position; *f*, filaments; *m*, connective (joining anther cells); *a*, *a′*, anther cells. *C*, the anthers and connectives bent into a horizontal position by an insect pushing against *a*. — After Lubbock.

407. Flowers with stamens and pistils each of two lengths. The flowers of bluets, partridge berry, the primroses, and a few other common plants secure cross pollination by having stamens and pistils of two forms (Fig. 333). Such flowers are said to be *dimorphous* (of two forms). In the short-styled flowers, *B*, the anthers are borne at the top of the corolla tube and the stigma stands about halfway up the tube. In the long-styled flowers, *A*, the stigma is at the top of the tube and the anthers are borne about halfway up. An insect pressing its head into the throat of the corolla of *B* would become dusted with pollen, which would be brushed off on the stigma of a flower like *A*. On leaving a long-styled flower the bee's tongue would be dusted over with pollen, some of which might readily be rubbed off on the stigma of the next short-styled flower that was visited. Cross pollination is insured, since all the flowers on a plant are of one kind, either long-styled or short-styled, and since the pollen is of two sorts, each kind sterile on the stigma of any flower of similar form to that from which it came.

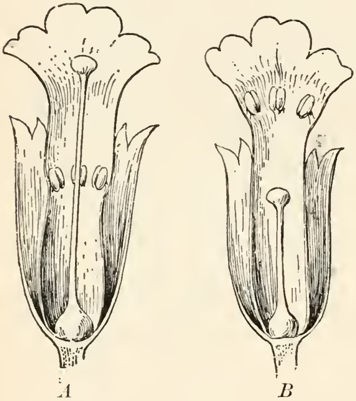

FIG. 333. Dimorphous flowers of the primrose

A, a long-styled flower; *B*, a short-styled one. — After Frank

Trimorphous flowers, with long, medium, and short styles, are found in a species of loosestrife and in the pickerel weed (*Pontederia*).

408. Cleistogamous flowers. In marked contrast with such flowers as those discussed in the preceding sections, which bid for insect visitors or expose their pollen to be blown about by the wind, are certain flowers which remain closed even during the pollination of the stigma. These flowers are called *cleistogamous* (meaning with shut-in fertilization) and are of course not cross-pollinated. Usually they occur on plants which also bear flowers adapted for cross pollination, and in this case the closed flowers are much less conspicuous than the others, yet

Fig. 334. A violet, with cleistogamous flowers

The structures which look like flower buds are cleistogamous flowers in various stages of development. The pods are the fruit of similar flowers. The plant is represented as it appears in late July or August, after the ordinary flowers have disappeared they produce much seed. Every one knows the ordinary flowers of the violet, but most people do not know that violets very generally, after the blossoming season (of their showy flowers) is over, produce many cleistogamous flowers, as shown in Fig. 334.

FIG. 335. Protection of pollen from moisture

At the left herb Robert and sweet scabious in sunny weather; at the right the same flowers during rain. — After Kerner

409. Protection of pollen from rain. Pollen is very generally protected from being soaked and spoiled by rain or dew by the natural position of the flower, which prevents rain from entering, as in the case of most sympetalous, nodding flowers, such as the lily of the valley and the flowers of the blueberry, huckleberry, wintergreen, and a multitude of others. Often, in two-lipped flowers, the anthers are more or less completely covered by the upper lip (Fig. 331). In the salver-shaped flowers, such as those of phlox, the mouth of the corolla tube is often so narrow that no rain or dew can enter it. Many corollas of the same general type as that of the sweet pea (Fig. 126) have the stamens covered by certain petals. A large number of flowers, such as the crocus, rose, pond lily, magnolia, and many heads, such as those of the dandelion, the chicory, and the hawkweed, close in wet weather and open in the sunshine. Sometimes the flower both changes its position and closes, as is the case with the common cranesbill, the herb Robert, and the sweet scabious (Fig. 335). In the linden and the jewelweed the flowers are covered by the foliage leaves of the plant so that rain can hardly ever enter them.

CHAPTER XXXIII

HOW PLANTS ARE SCATTERED AND PROPAGATED

410. Dispersal of plants by roots and rootstocks. Some of the highest spore plants, as the ferns, spread freely by means of their creeping rootstocks, and the gardener who wishes to get large strong ferns quickly often finds it the easiest plan to cut to pieces and reset the rootstocks of a well-established plant. In the walking fern (Fig. 273) the tip of the frond roots and begins a new plant. The student has learned (in Chapters IV and VI) that roots and underground stems of many kinds may serve to reproduce the plant. Either roots or rootstocks may travel considerable distances horizontally in the course of their growth and then shoot up and produce a new plant, which later becomes independent of the parent. The sedges (Fig. 44) are excellent illustrations of this process, and trees like the common locust and the silver-leaf poplar become great nuisances in the neighborhood of lawns and gardens by sending up sprouts in many places. When growing wild, such trees as these

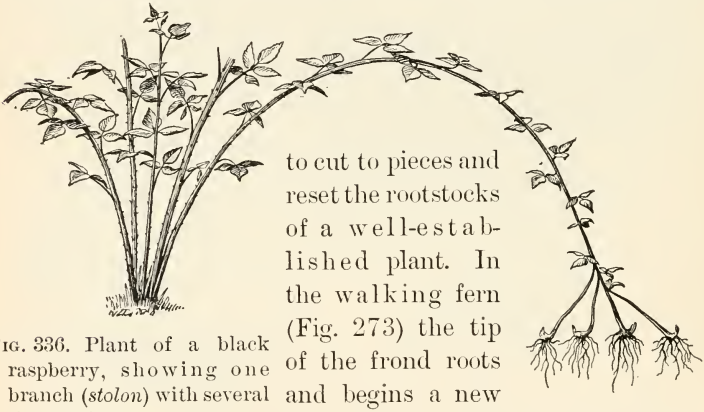

Fig. 336. Plant of a black raspberry, showing one branch (*stolon*) with several tips rooting

After Beal

depend largely upon propagating by the roots to keep up their numbers.[1]

411. Dispersal of seed plants by branches. There is a shrub of the honeysuckle family,[2] common in the northern woods, which is quite generally known as hobblebush, or witch-hobble, and sometimes as trip-toe. This is because the branches take root at the end and so form loops which catch the foot of the passer-by. The same habit of growth is found in the raspberry bush (Fig. 336), in one species of strawberry bush (*Euonymus*), and in some other shrubs. Many herbs, like the strawberry plant and the cinquefoil, send out long leafless runners which root at intervals and so propagate the plant, carrying the younger individuals off to a considerable distance from the parent.

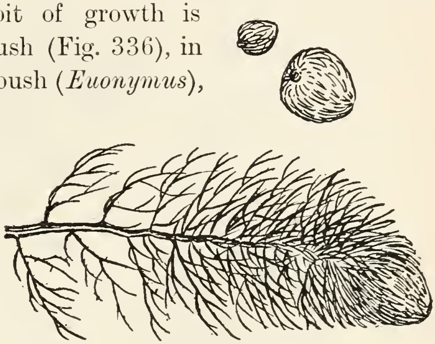

Fig. 337. A free branch and two buds of bladderwort

After Beal

Living branches may drop freely from the tree and then take root and grow, after having been blown, or carried by a brook or river, to a favorable spot, perhaps hundreds of yards away. The so-called snap willows lose many live twigs under conditions suitable for starting new trees.

A slightly different mode of dispersal from that of the raspberry is one in which buds separate from the plant and serve to propagate it. In the bladderwort (Fig. 337), at the close of the growing season, the terminal buds are released by the decay of the stem and sink to the bottom of the water in which the plants live, there to remain dormant until spring. Then each bud starts into life and gives rise to a new individual.

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[1] See Beal, *Seed Dispersal*, Chapters II and III.

[2] *Viburnum lantanoides.*

412. Dispersal of seed plants by bulblets. Almost every farmer's boy knows what "onion sets" are. This name is often given to little bulbs produced at the top of a naked flower stalk, or scape, by some kinds of onions which do not usually flower or bear seed. Tiger lilies produce somewhat similar bulblets in the axils of the leaves, and there is a large number of species, scattered among numerous families of plants, all characterized by the habit of producing bulblets or fleshy buds, borne on the stems or leaves above ground and of use in propagation. When mature the bulblets fall off readily, and if they find lodgment on unoccupied soil they grow readily into new plants. Sometimes they are carried moderate distances by wind or water,

FIG. 338. Fruit of smoke tree (*Rhus Cotinus*)

Only one pedicel bears a fruit, all the others are sterile, branched, and covered with plumy hairs and if the ground slopes they may easily roll far enough to get started in new places.

413. Dispersal of seeds. Seeds are not infrequently scattered by apparatus with the aid of which the plant throws them about. More commonly, however, they depend upon other agencies, such as wind, water, or animals, to carry them. Sometimes the transportation of seeds is due to the structure of the seeds themselves, sometimes to that of the fruit in which they are inclosed; the essential point is to have transportation to a long distance made as certain as possible, to avoid overcrowding.

414. Explosive fruits. Some dry fruits burst open when ripe in such a way as to throw their seeds violently about. Interesting studies may be made, in the proper season, of the fruits of the common blue violet, the pansy, the wild balsam, the garden balsam, the cranesbill, the herb Robert, the witch-hazel, the Jersey tea, and some other common plants. The capsule of the tropical American sand-box tree bursts open when throughly dry with a noise like that of a pistol shot. The explosive force of fruits is derived from the fact that some of their parts on drying are left in a state of tension, some layers of cells being compressed or stretched and tending to readjust their position.

Fig. 339. Fruits of linden, with a bract joined to the peduncle and forming a wing

415. Winged or tufted fruits and seeds. The fruits of the ash, box elder, elm, maple (Fig. 160), and many other trees are provided with an expanded membranous wing. Some seeds, as those of the catalpa and the trumpet creeper, are similarly appendaged. Winged fruits and seeds are borne on trees or shrubs, and the wing is usually so adjusted as to make its descent slow, with a spinning motion. As a rule, winged fruits and seeds are much heavier than those with a tuft of hairs. The fruits of the dandelion, the thistle, the fleabane, the arnica (Fig. 166, III), and many other plants of the group *Compositæ,* to which these belong, and the seeds of the willow, the milkweed, the willow-herb, and other plants, bear a tuft of hairs. All these seeds and fruits may in windy weather be seen traveling often to great distances.

Fig. 340. Russian thistle
After Dewey

416. Tumbleweeds. Late in the autumn, fences, particularly on prairie farms that are not carefully tilled, or in pastures, often serve as lodging places for immense numbers of certain dried-up plants known as tumbleweeds. These blow about over the level surface until the first snow falls and even after that (Fig. 341), often traveling for many miles before they come to a stop, and rattling out seeds as they go. Some of the commonest tumbleweeds are the Russian thistle (*Salsola Kali* var. *Tragus,* Fig. 340), the pigweed (*Amarantus albus,* Fig. 341), the tickle grass (Fig. 342), and a familiar peppergrass (*Lepidium*). In order to make a successful tumbleweed, a plant must be pretty nearly globular in form when fully grown and dried, must be tough and light, must break off near the ground, and drop its seeds only a few at a time as it travels. A single plant of Russian thistle is sometimes as much as three feet high and six feet in diameter, and carries not less than 200,000 seeds.

417. Many-seeded pods with small openings. There are many fruits which act somewhat like pepper boxes. The capsule of the poppy is a good instance of this kind, and the fruit of lily, monkshood (Fig. 159), columbine, larkspur, velvet leaf (*Abutilon Avicennæ*), and jimson weed (Fig. 343, *C*) acts in much the same way. Clamping the dry peduncle of any one of these ripe fruits, so as to hold it upright above the table top, and swinging it back and forth, will readily show its efficiency in seed dispersal.

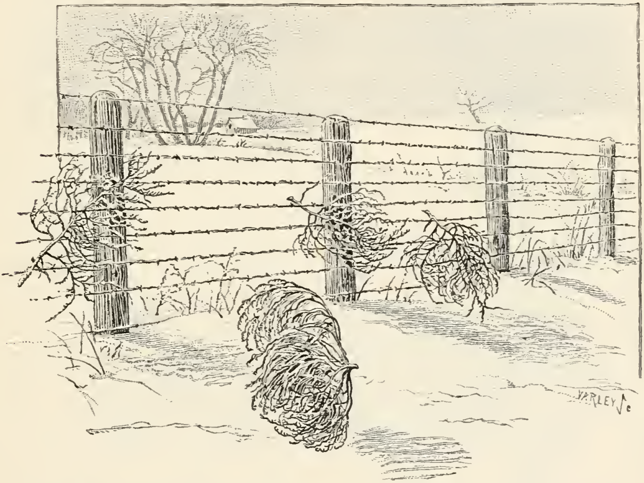

Fig. 341. Tumbleweeds[1] lodged against a wire fence in winter

After Millspaugh

418. Study of transportation by water. Nothing less than a long series of observations by the pond margin and the brookside will suffice to show how general and important is the work done by water in carrying the seeds of aquatics. Many plants usually have their seeds transported by water, and some appear to have no provision for dissemination in any other way.

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[1] *Amarantus albus.*

Ocean currents furnish transportation for the longest journeys that are made by floating seeds. It is a well-known fact that cocoa palms are among the first plants to spring up on newly formed coral islands. The nuts from which these palms grew may readily have floated a thousand miles or more without injury. On examining a cocoanut with the fibrous husk attached, just as it falls from the tree, it is easy to see how well this fruit is adapted for transportation by water. There are altogether about a hundred drifting fruits known, one (the Maldive nut) reaching a weight of twenty to twenty-five pounds.

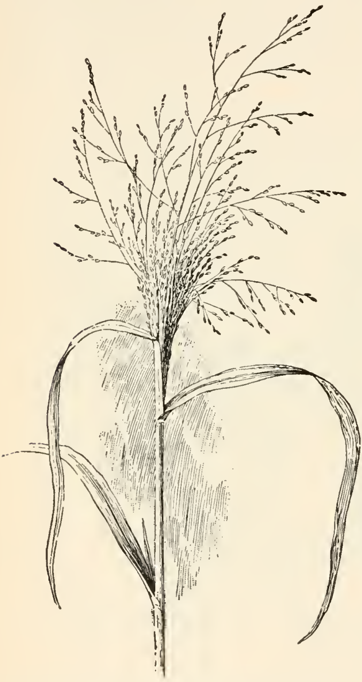

Fig. 342. Panicle of tickle grass, a common tumbleweed

After Host

419. Burs. A large class of fruits is characterized by the presence of hooks on the outer surface. These are sometimes outgrowths from the ovary, or the style (as in avens), sometimes from the calyx, sometimes from an involucre. Their office is to attach the fruit to the hair or fur of passing animals. Often, as in sticktights (Fig. 344 *A*, *B*), the hooks are comparatively weak, but in other cases, as in the cocklebur (Fig. 344 *D*), and still more in the *Martynia* (the fruit of which in the green condition is much used for pickles), the hooks are exceedingly strong. Cockleburs can hardly be removed from the tails of horses and cattle, into which they have become matted, without cutting out all the hairs to which they are fastened.

A curious case of distribution of this kind occurred in the island of Ternate, in the Malay Archipelago. A buffalo with his

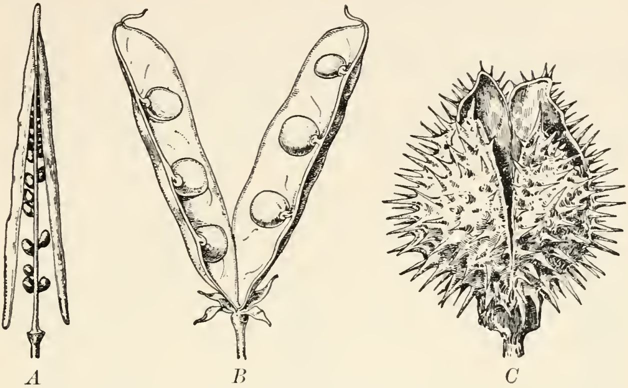

FIG. 343. Three fruits adapted for dispersal by the shaking action of the wind

A, celandine; *B*, pea; *C*, jimson weed (*Datura*). — After Decaisne

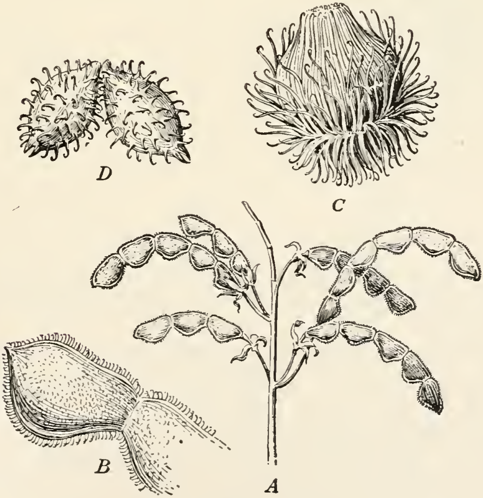

FIG. 344. Burs

A, sticktights; *B*, sticktights, two segments (magnified); *C*, burdock; *D*, cockleburs. — After Kerner hair stuck full of the needle-like fruits of a grass[1] was sent as a present to the so-called king of Ternate. Scattered from the hair of this single animal, the grass soon spread over the whole island.

420. Uses of stone fruits and fleshy fruits to the plant. Besides the *dry fruits*, of which some of the principal kinds have been mentioned, there are many kinds of *stone fruits and other fleshy fruits.* Of these the great majority are eatable by man or some of the lower animals, and oftentimes the amount of sugar and other food material which they contain is very considerable. It is a well-recognized principle of botany that plants do not make unrewarded outlays for the benefit of other species. Evidently the pulp of fruits is not to be consumed or

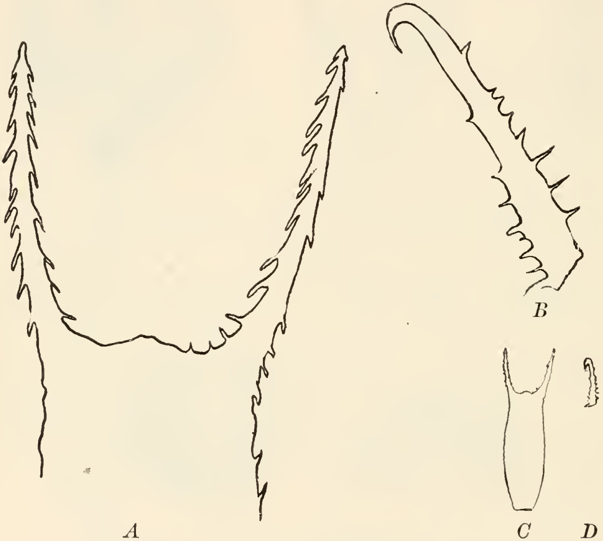

Fig. 345. Barbs and hooks of burs

A, barbed points from fruit of beggar's ticks, × 11; *B*, hook of cocklebur, × 11; *C*, beggar's ticks fruit (natural size); *D*, cocklebur hook (natural size)

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[1] *Andropogon acicularis.*

used as food by the plant itself or, in general, by its seeds. There are, therefore, several points to be explained on the basis of possible advantages to the plant. These are:

1. The eatable nature of the pulp of many fruits.

2. The bitter or other unpleasant taste of many seeds, as those of the orange and lemon.

3. The hardness or toughness of many seeds of pulpy fruits, as the date and the peach.

4. The small size and indigestibility of seeds of pulpy fruits, as the fig and the raspberry.

A little observation in the field suffices to show that most pulpy fruits are habitually eaten by birds or other animals large enough to carry them away from the parent plant. Seeds of disagreeable flavor, and very large hard seeds are often avoided by the animal in eating the fruit which contains them. Small hard seeds are commonly swallowed whole and frequently remain nearly unacted upon by the digestive fluids, so that they traverse the digestive tract of the fruit-eating animal which swallowed them and remain perfectly capable of germination. In this way such instances of dissemination as those of the raspberry (Fig. 346) and the red cedars (Fig. 347) are readily explained.

Fig. 346. Red raspberry bush, in fork of a maple

421. Seed carrying purposely done by animals. In the cases referred to in the preceding sections, animals have been seen to act as unconscious or even unwilling seed carriers. Sometimes, however, they carry off seeds with the plan of storing them for food. Ants drag away with them to their nests certain seeds which have fleshy growths on their outer surfaces. Afterwards they eat these fleshy parts at their leisure, leaving the seed perfectly fit to grow, as it often does.[1]

Fig. 347. Red cedar trees planted by birds roosting on fences

After Pinchot

Squirrels and blue jays are known to carry nuts and acorns about and bury them for future use. These deposits are often forgotten and so get a chance to grow, and in this way a good deal of tree planting is done.

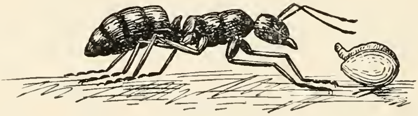

Fig. 348. Seed of bloodroot with caruncle, or crest, which serves as a handle for ants to hold on to. Ant ready to take the seed

After Beal

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[1] See Beal, *Seed Dispersal*, pp. 69, 70.

CHAPTER XXXIV

SOCIAL HABITS OF PLANTS; COMPETITION AND INVASION

422. Social habits. Those plants which live associated with many individuals of the same species are called *social* plants. Those kinds which are not social usually occur as members of *plant communities*, or assemblages of two or more species. The vegetation of the earth mainly consists of such assemblages, and the total number of solitary plants is comparatively small.

Adult seed plants are usually incapable of locomotion, and only a small proportion of all the kinds of seeds (though a somewhat larger proportion of fruits) is equipped with means for carrying them on long journeys. It is therefore natural that the offspring of any plant or plant community should generally be found near the parent plants. It is not easy to trace the working of this gradual spread of the successive broods in the neighborhood of the parents where there is already dense vegetation. But in any region where there are considerable areas destitute of any given vegetation form, as in cleared land, the young seedlings of an oak, a hickory, or a black walnut may often be detected in many places near the parent tree.

423. Competition. Every one knows, in a general way, that in a state of nature plants often greatly crowd each other. This is evident enough from mere inspection of most meadows, thickets, or tracts of woodland or waste land; but in order to realize how few of all the bidders for each square foot of ground actually find a chance to occupy it, a little calculation is needed. A single annual seed plant usually matures hundreds and often thousands of seeds. One common weed of the Middle West, the Russian thistle[1] (Fig. 340), often produces as many as 25,000

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[1] *Salsola Kali* var. *Tragus.*

seeds and occupies as much as four square feet of earth. The offspring of an individual of this species, therefore, if all the seeds grew to mature plants, would cover nearly 2.3 acres. It may interest the student to calculate in what generation the descendants of one plant would cover the entire area of his state.

424. Statistics of overcrowding. Charles Darwin seems to have been one of the earliest observers, if not the very first, to collect exact statistics in regard to the severity of competition among plants. He found that out of 20 species which occurred on a plot of turf three by four feet in area nine species died from overcrowding by the others. On a piece of dug and cleared ground he found that 60 weed seedlings to the square foot sprang up and 49 of them were destroyed, chiefly by slugs and insects.[1]

In a rich and weedy bit of land Professor L. H. Bailey found in an area of twenty by twenty square inches ten species of weeds. Reduced to the number per square foot, there were: July 10, 30 plants; August 13, 31 plants; September 25, 25 plants. Several of these were large weeds, such as the redroot (*Amarantus retroflexus*) and the ragweed (*Ambrosia artemisiæfolia*).

On June 23 of the next year there were on the same plot (which had remained undisturbed) eleven species, numbering 108 plants to the square foot, and now the dominant plants were red clovers. Most of the other plants were puny and suffering from lack of light under the shade of the clovers.[2]

If one selects a plot in which seedlings are just starting, the number of individuals to the square foot will often be found to be much greater than those above given. Under a full-grown tree of the wild black cherry the writer has found on June 9 portions of the ground containing hardly any other seed plants except cherry seedlings at the rate of 104 to the square foot. Not one of all the thousands which had begun to grow could

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[1] *Origin of Species*, Chapter III.

[2] *The Survival of the Unlike*, pp. 258–261.

ever have developed into a full-sized individual on account of the overshadowing from the parent tree

In a weedy bit of lawn, where the grass had largely been killed by trampling and other disturbing causes, the writer found on June 9 plants at the rate of 1032 to the square foot as follows:

Plantain (*Plantago Rugelii*)	811
Grass (various species)	200
Knotgrass (*Polygonum aviculare*)	18
Sorrel (*Oxalis corniculata* var. *stricta*)	3
	1032

FIG. 349. Effect of competition on radishes

Both plants were grown from the same seed and in the same soil, planted at the same time. *A* was one of a lot standing so close together that their tap roots nearly touched one another; *B* had several square feet of ground to itself. About one-quarter natural size

The majority of the grass plants were apparently seedlings of the preceding autumn, and the plantains were young seedlings, most of them an inch or less in height. A full-grown plantain of this species occupies not less than 100 to 150 square inches, so that of these alone more than 800 individuals were likely to die of overcrowding.

425. How overcrowding kills. Of plants grown too close together many die and others are dwarfed (Fig. 349) and partially or wholly fail to flower or seed. This is one of the first lessons which the beginner in gardening learns, if he neglects properly to thin out his beds. Corn grown in closely planted drills for fresh fodder or ensilage makes few ears, and none of these are perfect. The weakening or destruction due to overcrowding results mainly from these three causes[1]:

1. Insufficient light and heat for plants shaded by their more vigorous neighbors, resulting in imperfect photosynthesis.
2. Scanty water supply, because most of the water is absorbed by the more vigorous root systems of the stronger individuals.
3. Deficient supply of dissolved salts (nitrates, phosphates, and so on), on account of their being largely consumed by the stronger plants.

426. Competition most fatal between similar plants. For obvious reasons, plants of the same general form and mode of growth usually interfere most with each other, and plants which are decidedly unlike interfere less, or even in some cases benefit each other. This principle is unconsciously followed, in many instances, by farmers and gardeners, as in the case of lawns sown with mixed grass seed, which produce a more perfect turf than those sown with a single species of grass. So, too, pumpkins are often planted in cornfields, and in southern Europe beans are raised in vineyards, in the partial shade of the vines.

If the interests of two or more kinds of plants occupying the same area conflict little or not at all, this may be due not only to their unlikeness of form or of requirements as regards light,

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[1] As far as terrestrial seed plants are concerned.

heat, or water, but also to their flowering and seeding at different seasons. Many kinds of weeds flourish in grainfields, making little growth until the grain is reaped, after which they develop rapidly and flower and seed among the stubble.

427. Invasion. Some of the ways in which plants are dispersed have already been described (Chapter XXXIII). The result of carrying seeds or other reproductive parts into new territory is to cause an *invasion* of that area. If the invaded ground contains no vegetation, the newcomers take full possession. Such a case occurs when the bed of a newly drained lake or bayou, or soil uncovered by landslides, or newly cooled material from volcanic eruptions is populated by vegetation brought in by natural agencies. If the invading species encounter other occupants of the region invaded, the new arrivals may simply share the territory with its previous occupants. But if the immigrants are much better adapted to the conditions of existence in the disputed area than are its actual occupants, the intruders may drive out all before them.

428. Native species ousted by invaders. New Zealand and the pampas of La Plata and Paraguay, in South America, have, during the nineteenth century, furnished wonderful examples of the spread of European species of plants over hundreds of thousands of square miles of territory. The newcomers were more vigorous, or in some way better adapted to get on in the world, than the native plants which they encountered, and so managed to crowd multitudes of the latter out of existence.

In our own country a noteworthy case of the kind has occurred so recently that it is of especial interest to American botanists. The so-called Russian thistle (Fig. 340), which is merely a variety of the saltwort common along the Atlantic coast, was first introduced into South Dakota in flaxseed brought from Russia and planted in 1873 or 1874. In twenty years from that time the plant had become generally distributed as one of the commonest weeds over an area of about 25,000 square miles.

American plants, on the other hand, have in many cases overrun other countries. *Elodea*, a common water weed with us, introduced into Great Britain about 1847, now chokes up many pools and water courses in England and Scotland. The prickly pear cactus (*Opuntia Ficus-indica*) and the century plant, both emigrants from North America, are now the most conspicuous plants along many cliff sides all over southern Italy. A prickly pear has become such a nuisance in New South Wales that large rewards are offered for its extermination.

429. Weeds. Any flowering plant which is troublesome to the farmer or gardener is commonly known as a weed. Though such plants are annoying from their tendency to crowd out others useful to man, they are of extreme interest to the botanist on account of this very hardiness. The principal characteristics of the most successful weeds are their ability to live in a variety of soils and exposures, their rapid growth, resistance to frost, drought, and dust, their unfitness for the food of most of the larger animals, in many cases their capacity to accomplish self pollination, in default of cross pollination, and their ability to produce many seeds and to secure their wide dispersal.

Sometimes the seeds have great vitality; those of shepherd's purse and purslane are capable of germinating after fifteen years or more. Many of the worst weeds, such as sow thistle,[1] sorrel,[2] witch grass,[3] nut grass,[4] and field garlic,[5] have creeping rootstocks or bulbs or tubers. Not every weed combines all of these characteristics. For instance, the velvet leaf, or butter print, common in cornfields, is very easily destroyed by frost; the pigweed and purslane are greedily eaten by pigs, and the ragweed by some horses. The horse-radish does not usually produce any seeds, but is propagated by vegetative methods.

It is a curious fact that many plants which have finally proved to be noxious weeds have been purposely introduced into the country. The fuller's teasel, melilot, horse-radish, wild

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[1] *Sonchus.* [2] *Rumex.* [3] *Agropyrum.* [4] *Cyperus.* [5] *Allium.*

carrot, wild parsnip, tansy, oxeye daisy, and field garlic are instances of this.

430. Origin of weeds.[1] By far the larger proportion of our weeds are not native to this country. Some have been brought from South America and from Asia, but most of the *introduced* kinds come from Europe. The importation of various kinds of grain and of garden seeds, mixed with seeds of European weeds, will account for the presence of many of the latter among us. Others have been brought over in the ballast of vessels. Once landed, European weeds have succeeded in establishing themselves in so many cases, because they were superior in vitality and in their power of reproduction to our native plants. This may not improbably be due to the fact that the European and western Asiatic vegetation, much of it consisting from very early times of plants growing in comparatively treeless plains, has for ages been habituated to flourish in cultivated ground and to contend with the crops which are tilled there.

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[1] See the article, "Pertinacity and Predominance of Weeds," in *Scientific Papers of Asa Gray*, selected by C. S. Sargent, Vol. II, pp. 234–242.

CHAPTER XXXV

PLANT SUCCESSIONS *

431. Nature of plant successions. Whenever a portion of the earth's surface is stripped of its vegetation, or undergoes any decided change in its physical condition, the way is usually opened for invasion of plants from the surrounding territory (Sec. 427). In most cases the immigrants are not all of them thoroughly adapted to their new home, and cannot become so; or the condition of the territory may continue to change, so that a series of new populations appears, each in turn wholly or partly giving way to that which follows it. Such a set of colonizings is called a *plant succession.*

432. Causes of successions. It would require too much space to state more than a very few of the causes which originate plant successions.

First. They may be brought about by the introduction into a region of new species which are able, without change of soil or climate, to drive out some or all of the original occupants (Sec. 428).

Second. They may be brought about by changing the supply of light, heat, water, or other important factors in the surroundings of the plant. Such changes are sometimes natural, sometimes produced by man.

Such a river as the Mississippi, with over 12,000 square miles in its delta, affords a good instance of the power of natural agencies to alter the conditions of plant life. Perhaps one third of the delta is a sea marsh, with the vegetation characteristic of

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* To the Instructor: As this chapter is somewhat more technical than many of the others of Part III, it may be omitted if limitations of time demand a briefer course.

shallow, salt, or brackish water in a warm-temperate climate, while the remaining portion supports in places a most luxuriant growth of land plants. Year by year, along the margin of the submerged part of the delta, as this emerges from the water, the change from aquatic to land vegetation goes on, and year by year the flora which first establishes itself in the newly emerged mud is succeeded by others more adapted to ordinary soil.

Fig. 350. Aspen succession after forest fires in coniferous woods, Colorado

After Clements

Man produces most extensive changes in vegetation by such operations as draining lakes and swamps, building levees, irrigating deserts and semi-deserts, clearing woodlands, and planting treeless lands with the seeds of forest trees.

433. Order of succession in special cases. Much study has recently been given to the exact order in which assemblages of plants follow each other in various kinds of succession. Only a very few cases can here be mentioned.

On the island of Krakatoa, which was completely laid waste by a volcanic eruption in 1883, the first forms of plant life to appear were microscopic blue-green algæ (Secs. 207–211). Three years after the eruption the flora had come to contain many ferns, with here and there a few seed plants, on the mountains or the coast.

In the mountains of Colorado the granite bowlders dislodged from the faces of cliffs are covered first with incrusting lichens; then the gravel produced by the weathering of the granite gives a footing to leaf-like lichens; later the more weathered gravel supports a growth of herbaceous seed plants; afterward follow thickets, then pine forests, and finally spruce forests (Plate XII).

In the pine woods[1] of central Maine when the trees have been cut away and the clearing (as is too often the case) burned over, the most conspicuous plants which immediately succeed the forest are fireweed,[2] raspberries, blackberries, wild cherries,[3] and aspens.[4] A deciduous forest of poplars and canoe birches[5] succeeds the thickets above-mentioned. This in turn would doubtless, under natural conditions, after a long period, be displaced by a pine forest.

In eastern Maine the succession is very similar, except that blackberries are not common in the burned clearings and the tree growth which follows the thicket stage is usually of gray birch.[6]

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[1] *Pinus Strobus.*

[2] *Epilobium angustifolium.*

[3] *Prunus pennsylvanica.*

[4] *Populus tremuloides.*

[5] *Betula papyrifera.*

[6] *B. populifolia.*

434. Reasons for order of succession. It is not always possible to explain in detail why each set of plants in a succession takes possession of the ground and later on is itself driven out. In a general way it is clear that very low spore plants can make a living on bare rock surfaces or on partly decomposed rock where seed plants would find too little available salts, especially nitrates, to support their nutrition.

FIG. 351. Young black oaks succeeding loblolly pine and shortleaf pine, southeastern Texas

After von Schrenk

On lands where cultivation is abandoned, or which are in other ways suddenly exposed to invasion, weeds of many species often obtain a footing and flourish for some years before the truly wild native plants of the region take final possession. This is, in part at least, on account of the remarkable capacity of most weeds to seed themselves (Sec. 429).

Forest or grass land is the final stage in many successions. The former gains supremacy over the weedy thickets out of which it rises by shading the shrubs and herbs beneath the tree tops until all those not adapted to life in deep shade are destroyed. Grasses have to an unsurpassed extent the power of living with their roots (and sometimes also rootstocks) interwoven in a way which would prove fatal to most herbs. In this way a lawn or meadow, on good ground, may be seen to improve itself by choking out other plants which occur here and there among the grass. Salt marshes, with a comparatively scanty vegetation, are often purposely shut away from the sea, so that the rains can wash the excess of salt out of the soil. In four or five years they become thoroughly self-sown with the seeds of cultivated grasses and are changed into highly productive meadows.

CHAPTER XXXVI

ECOLOGICAL GROUPS AND THEIR CHARACTERISTICS *

435. Ecological grouping of plants. The ordinary classification of plants, as set forth in Part II, is based, as far as possible, on their actual relationships to each other. But when plants are considered ecologically they are grouped according to their relations to the world about them. They may, therefore, be gathered into as many (or more than as many) different groups as there are important factors influencing their modes of life. We may, for instance, classify plants as light-loving and shade-loving, and so on.

The most important consideration in classifying seed plants on ecological grounds is based on their requirements in regard to water. Grouped with reference to this factor in their life all plants may be designated as:

1. *Hydrophytes*, or water-inhabiting or water-tolerating plants.
2. *Xerophytes*, or drought-tolerating plants.
3. *Mesophytes*, or plants which thrive best with a moderate supply of water.

These three groups do not fully express all the relations of plants to the water supply, so two others are found convenient:

4. *Tropophytes*, or seasonal plants which are hydrophytes during part of the year and xerophytes during another part.[1]
5. *Halophytes*, or salt-marsh plants and "alkali" plants, species which can flourish in a very saline soil.

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* To the Instructor: If it is necessary to shorten the treatment of this subject, the latter part of the chapter, beginning with Sec. 442, may be omitted.

[1] The plants which E. Warming, one of the foremost authorities, classes as mesophytes are many of them grouped by another great authority, A. F. W. Schimper, as tropophytes.

436. Difficulties in ecological grouping. It seems at first sight a simple matter to group plants in regard to their need of water. There can be no difficulty in recognizing as hydrophytes all plants like the bladderworts, water cresses, certain mosses, and most algæ which live only in water. Cactuses, aloes, and similar plants are recognized at sight as xerophytes. But the chief difficulty is in dividing mesophytes from the other two assemblages, into which they shade by indefinite gradations. In a single mesophytic thicket, for example, one may find such hydrophytes as the pepper bush (*Clethra*) and such moderate xerophytes as the catbriers (*Smilax*). In order to know whether the plants of a region have plenty of water or not, we must know not only how many inches of yearly rainfall there are, but also what the soil is like, what is the temperature of the soil and air, whether or not there are dry winds, and whether there are fogs or heavy dews. A lichen on a bare rock may be living almost under desert conditions, while a pitcher plant in a bog near by has its roots in standing water (or in ice) nearly all the year round.

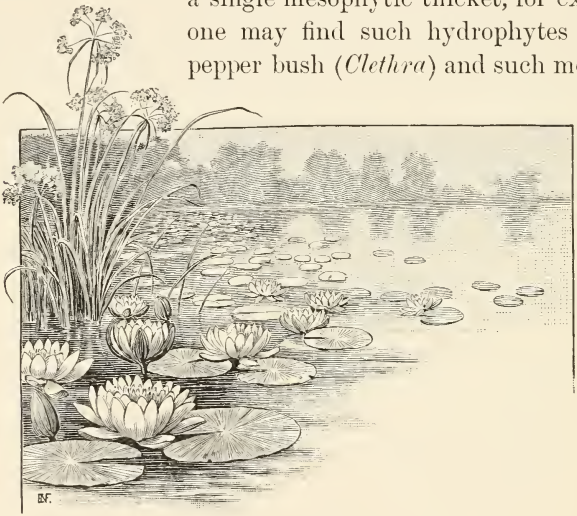

FIG. 352. Aquatic plants: pond lilies with floating leaves, and sedges with aërial leaves

437. Hydrophytes. Some of these are herbaceous aquatic plants, like the duckweed, the pickerel weed, the pond lily, and the water crowfoot; others, such as the cultivated "calla" (*Richardia*), the buck bean, the cat-tail, and the sweet flag, many ferns, mosses, and liverworts, prefer damp air and soil. All of them transpire freely, and many of them cannot live at all under the moisture conditions which suit ordinary plants.

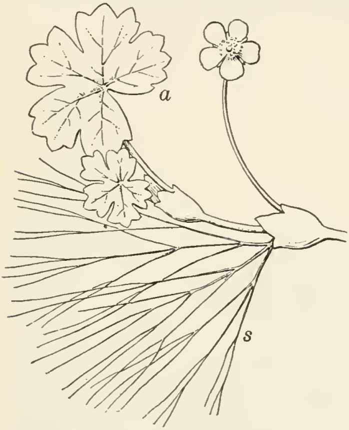

Fig. 353. Submerged and aërial leaves of a crowfoot (*Ranunculus aquatilis*)

The leaf with thread-like divisions is the submerged one. — After Giesenhagen

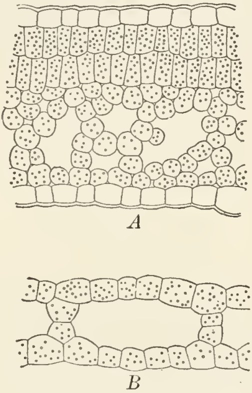

Fig. 354. Cross sections of leaves of arrowhead (*Sagittaria*)

A, aërial leaf; *B*, submerged leaf. The submerged leaf has no ordinary epidermis and no palisade layer, but large air spaces. Much magnified. — After Bonnier and Sablon

Some aquatics have their leaves wholly submerged, others, such as the duckweed (Fig. 355) and the pond lilies (Fig. 352), have them floating, and still others, like the sedges in the same illustration, have their leaves freely exposed to the air. A few plants have both water leaves and air leaves (Fig. 353). Some aquatic plants are rooted in the mud, while others have no roots at all, or, like the duckweed, have only water roots.[1]

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[1] See grouping in Sec. 454.

The leaves of land plants in very rainy sub-tropical climates are exposed to the attacks of parasitic fungi. To ward off the attacks of these and to allow free transpiration, it is necessary to keep water from accumulating on the surfaces of the leaves. This result is secured by a waxy deposit on the epidermis, and also by the slender prolongation to drain off surplus water, shown in Fig. 356. That this slender leaf tip is useful in the way suggested is proved by the fact that when it is cut squarely off the leaf no longer sheds water freely.

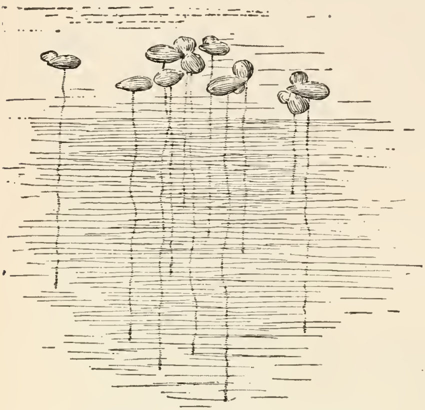

Fig. 355. The duckweed, a floating aquatic plant

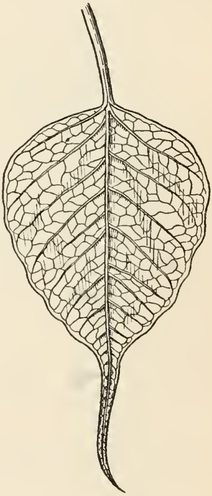

Fig. 356. Leaf of an East Indian fig tree,[1] with a slender, tapering point to drain off water

After Schimper

438. Xerophytes. A *xerophyte* is a plant which is capable of sustaining life with a very scanty supply of water. Since the first plants which existed were aquatics, we must consider that xerophytes are highly specialized and modified forms adapted to extremely trying conditions of life. A typical xerophyte is one which can live in a very dry soil in a nearly rainless region. The yucca and the cactuses (Figs. 50, 357) are good examples of such plants. Less extremely xerophytic are plants like the date palm (Fig. 53), which flourishes in the

[1] *Ficus religiosa.*

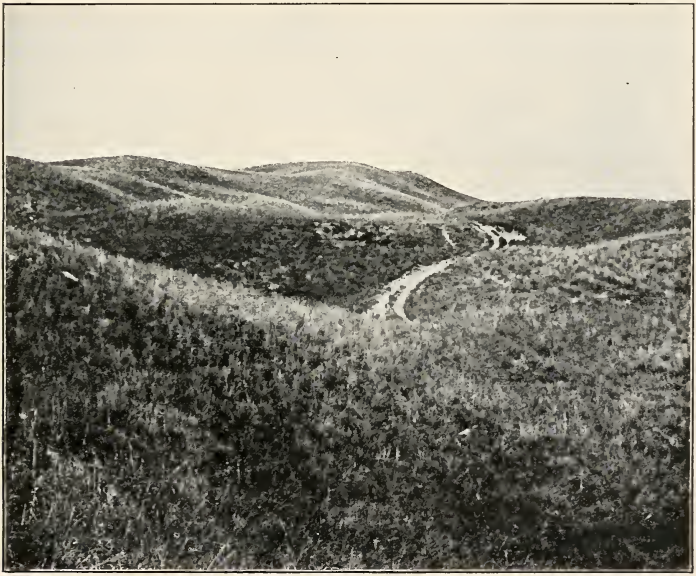

Plate IX.

The upper picture shows a belt of trees along a Nebraska river

After U. G. Cornell

The lower picture shows xerophytic grasses on Nebraska sand hills

After R. A. Emerson

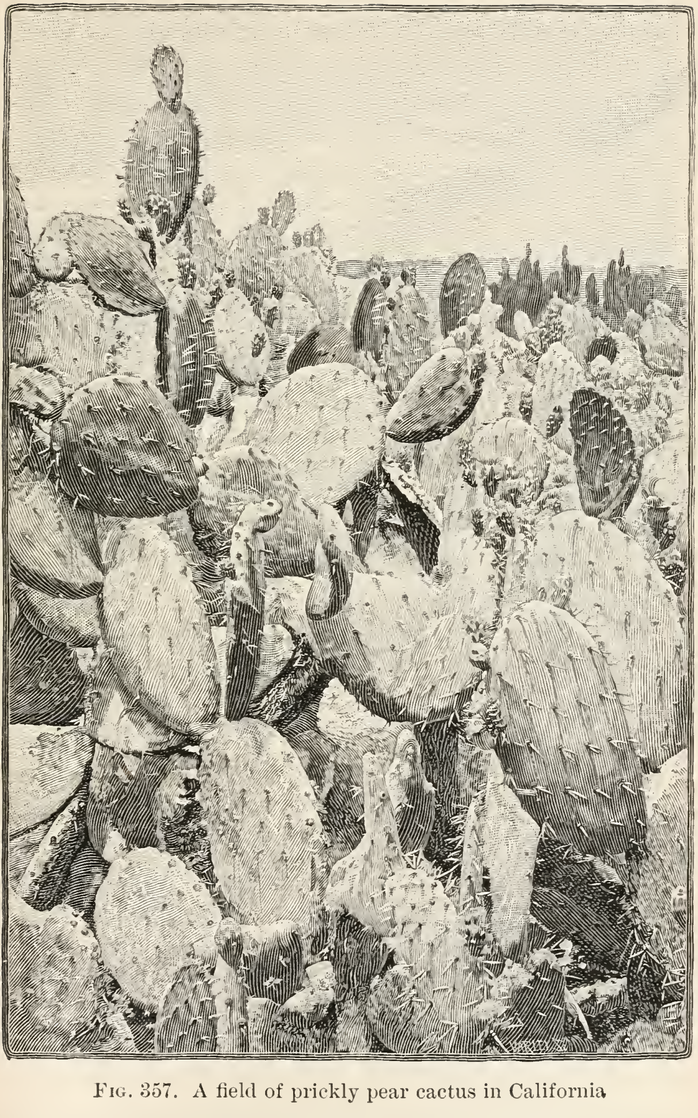

FIG. 357. A field of prickly pear cactus in California

oases of the Sahara, where the soil is moist from the presence of springs, though rains are almost unknown, or the houseleeks and stonecrops found in many gardens, the so-called Spanish moss (Plate III), and lichens (Figs. 226, 227), all of which grow most rapidly in moist air, but cling to bare rocks and trunks of trees, from which they get no water.

Fig. 358. *Harpagophytum*, a South African xerophyte

After Schimper

It is important to notice that *many xerophytes only economize water when forced to do so.* With an abundant supply of water they may transpire almost or quite as much as mesophytes. But a drought which would kill the latter would only cause the xerophytes to close their stomata and greatly lessen transpiration. A xerophyte must be capable of storing water and transpiring very slowly, like cactuses, aloes, stonecrops, and such fleshy plants with a thick epidermis, or else it must be able to revive after being thoroughly dried.

439. Roots and stems of xerophytic seed plants. Some xerophytes have roots which show no peculiarities of form or structure, but many make special provision for storing food and water in their roots. Such roots are fleshy and often, as in *Harpagophytum* (Fig. 358), are of great size compared with the portion of the plant above the ground. Xerophytic stems are frequently very thick in proportion to their length, sometimes even globular (Fig. 50), and they commonly contain large amounts of water. In leafless plants, like the cactuses, the surface for transpiration is much less than that offered by leafy plants. Many species which bear leaves shed most of them at the beginning of the dry season, and some remain thus in a half dormant condition for long periods, as is the case with many *Euphorbias* (Fig. 318).

The epidermis, even on the younger portions of the stem, is highly cutinized, and this structure makes any evaporation very slow.

440. Leaves of xerophytes. Since the leaf is in general the main organ of transpiration, we might expect to find the leaves of xerophytes highly adapted to their environment. This is the case, and some of their principal means of protection from excessive transpiration are as follows[1]:

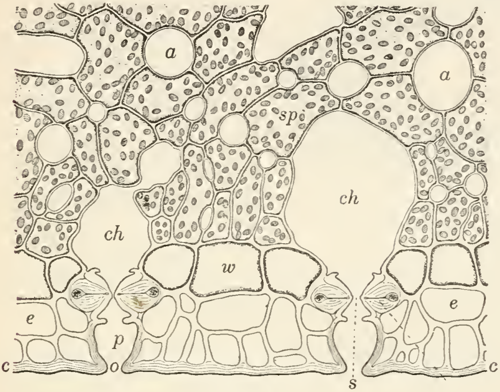

Fig. 359

Fig. 360

Fig. 359. Cross section of leaf of *Ficus elastica*

c, cuticle; *o*, opening to pit; *p*, pit leading to stoma; *s*, stoma; *e*, epidermal cells; *w*, special cells for storage of water; *ch*, air chamber from stoma; *sp*, cells of spongy parenchyma; *a*, intercellular air spaces. Much magnified

Fig. 360. Fleshy leaves of Mesembryanthemum, with stored water

After Giesenhagen

1. A thick epidermis, often of several layers of cells (Fig. 359).
2. Storage of water in epidermal cells.
3. Small stomata, often deeply sunken (Fig. 359).
4. Epidermal hairs or scales. These are often extraordinarily abundant, and in some cases give one or both surfaces of the leaf a silky or silvery luster.

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[1] See Warming, *Lehrbuch der Œkologischen Pflanzengeographie, vierter Abschnitt*, Berlin, 1902.

5. Coatings of wax or varnish or incrustations of salts.
6. Extreme development of the palisade layer.
7. Reduction of the intercellular spaces.
8. Mucilaginous, water-retaining cell contents in the spongy parenchyma of the leaf (usually in fleshy leaves, Fig. 360).
9. Permanent vertical position of leaves (Figs. 45, 110, 111).
10. Leaf movements, presenting only the edges to the sun during the heat of the day (Sec. 114).

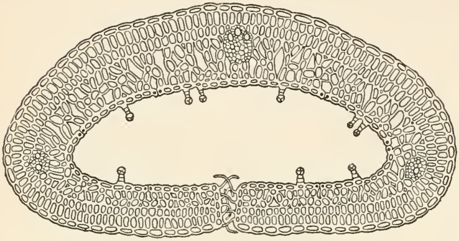

FIG. 361. Cross section of rolled-up leaf of crowberry (*Empetrum nigrum*)

Magnified. — After Kerner

11. Rolling up of leaves, either permanent, as in Fig. 361, or temporary, as in Indian corn and in Fig. 362.

12. Reduction of leaf area, — the leaves either few or small, or both. Sometimes the leaf consists of little else besides a petiole; sometimes, as in Figs. 50 and 357, foliage leaves are wholly absent.

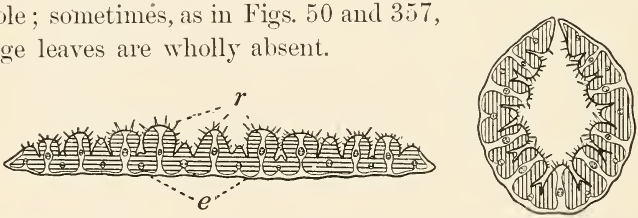

FIG. 362. Cross section of leaves of a grass,[1] unrolled for exposure to sunlight and rolled up to prevent evaporation

r, ridges of the upper epidermis, with many stomata on their surfaces; *e*, thick lower epidermis, without stomata. — After Kerner

In regions with a long rainless summer, like that of southern California or the coast of the Mediterranean, many shrubs are summer deciduous, and in their leafless condition the twigs

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[1] *Stipa capillata.*

have been found to transpire less than 3 per cent of their maximum rate when leafy.

Some of the principal differences between hydrophytes and xerophytes may be summed up as follows:

	HYDROPHYTES	XEROPHYTES
Roots	Few	Many
Water-conducting tissue	Scanty	Abundant
Air-conducting tissue	Abundant	Scanty
Water-storage tissue	Wanting	Often abundant
Epidermis	Thin or wanting	Thick
Leaves	Often large or dissected	Usually of reduced surface

441. Mesophytes. A mesophyte is a plant which thrives best with a moderate supply of water. The great majority of the wild and the cultivated plants of the United States are mesophytes. What has been learned from Part I of this book about the forms, structure, and habits of ordinary plants, together with what the student's own observation, aside from the study of botany, has taught him, should suffice to give him a fair idea of mesophytic plant life.

It is important to notice that most of our mesophytic trees and shrubs pass the winter (or in the extreme Southwest the dry season) in a leafless condition, and so transpire very little. So, too, our mesophytic, herbaceous perennials, such plants as the jack-in-the-pulpit, lilies, irises (Fig. 45), violets, and others. lose a large portion of their evaporating surface during part of the year by dying to the ground and leaving only the buried bulbs, roots with buds at the crown, or rootstocks alive.

All of the plants which make decided preparations for the season when water is hard to get may be classed as tropophytes or periodic xerophytes.

442. Deciduousness an acquired habit. The practice of shedding the leaves before the arrival of severe freezing weather, when it becomes almost impossible to draw moisture from the earth, or before the culmination of the severest drought of summer, may be regarded as a habit gradually acquired by deciduous trees and shrubs for their own protection. The duration of the period of leaflessness depends on the length of the dangerous season. Grapevines, for instance, in central Europe are leafy during about six months and leafless during the following six. But near Cairo, Egypt, the leafless period is only two months long, and in very warm and moist climates the vines are evergreen. So, too, cherry trees are evergreen in Ceylon, and beeches in Madeira.

A large shrubby *Euphorbia*,[1] common in southern Italy, is found absolutely leafless during July and August, when growing on the faces of limestone cliffs. But in moist soil, within a stone's throw of the leafless plants, there may be found others profusely leafy.

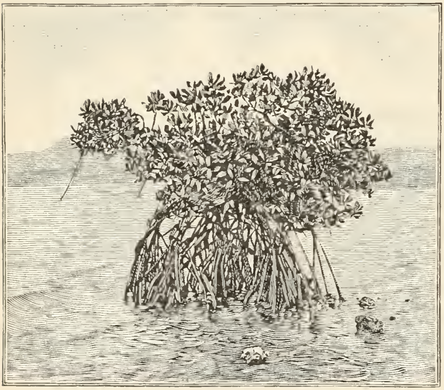

Fig. 363. The mangrove, a halophyte
After W. M. Davis

443. Halophytes. A halophyte is a plant which can thrive in a soil containing much common salt or other saline substances. The seaside is the principal region of halophytic vegetation, but many halophytic plants are also to be found in the neighborhoods about salt springs and the "alkali" lands of the Southwest and the Pacific slope.

The mangrove tree (Fig. 363) is one of the most remarkable of halophytes. It grows in shallow water along the seashore, and sends out many aërial roots which at length find their way down into the salt mud. In this way it collects drift material and gradually extends the shore line farther out to sea.

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[1] *E. dendroides.*

444. Form and structure of halophytes. Most halophytes present certain peculiarities of form and structure, such as succulence of stem or leaves, or both, a highly developed palisade layer, small intercellular spaces, diminution of evaporating surface, and often specially developed tissue for storage of water. These are evidently xerophytic characteristics, and their presence may be due to two causes:

First, the occurrence of salt in the soil renders absorption of the soil water comparatively difficult, since osmosis takes place more readily between nearly pure water and the liquid contents of the young roots and root hairs than between salt water and the liquids within the root. Halophytes may therefore be on a short allowance of water even when their roots are constantly wet.

Second, the absorption of much salt would poison the plant, and therefore it is an advantage to keep down transpiration and with it the rate at which salt water is allowed to enter the roots.

445. Halophytes not dependent on salts. It is worth while to note the fact that halophytes are not usually dependent on a highly saline soil. They are salt tolerators rather than salt lovers.[1] But they flourish in saline localities because they are capable of enduring much more salt than ordinary plants, and so can grow in salt marshes and such localities comparatively unhindered by the competition of non-halophytic species.

446. Other kinds of ecological classes. One may class plants with reference to their habits in many other regards than according to their relative economy of water or their tolerance of salts. Only one other kind of classification need, however, be mentioned in this chapter,— that is, the division into sun-loving and shade-loving plants. Even in very dense forests some plants are found growing on the soil in the twilight formed by the shade of the trees. Some of this undergrowth is of seed plants,

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[1] Or, in technical terms, the plants which grow in saline soils are *facultative* halophytes but not *obligate* halophytes.

and there are many ferns and mosses which flourish in such situations. Shade plants commonly have large pale leaves, and generally (except in ferns) the leaves are not much cut or lobed (Fig. 364, *A*). Sun-loving plants, on the other hand, usually have comparatively little leaf surface, and the leaves are often cut into narrow divisions (Fig. 364, *B*). Apparently the broad leaf surfaces in the one class are to expose many green cells to the light for starch making, while in the other class the slender leaf divisions expose enough assimilating cells, and at the same time the narrowness of the division permits plenty of light to penetrate to the plant's lower leaves. It is also, doubtless, much easier for leaves like those of the yarrow, the dog fennel, the tansy, the carrot, and their like to withstand the action of severe winds, to which they are often exposed, than it would be for leaves like those of the jack-in-the-pulpit, the trilliums, the lily of the valley, and similar leaves.

FIG. 364

A, a shade plant (*Clintonia*); *B*, a sun plant, dog fennel (*Maruta*)

447. Sun leaves and shade leaves on the same plant. On plants of the same species, or even on the same individual, sun leaves and shade leaves often differ widely. On comparing the leaves from the exterior and the interior of the crown of a deciduous tree, or such an evergreen species as the live oak or the olive, the sun leaves are usually found to be lighter-colored, of smaller area, thicker, and of more xerophytic structure than the shade leaves. The difference in size may be very great, the smallest sun leaves sometimes not covering more than a tenth of the area of the largest shade leaves on the same plant. There is usually, also, a notable difference in the form of the two kinds, the sun leaves being narrower in proportion to their length. Sun leaves are often several times as thick as shade leaves, and have far more completely developed palisade layers. The latter may even (in leaves grown in dense shade) be quite lacking, and the regular palisade cells be replaced by loosely arranged, funnel-shaped cells, with their broader ends toward the epidermis. Sun leaves have a much stronger fibro-vascular framework than those developed in a comparatively feeble light. In the case of plants which have the leaves more or less hairy or scaly, the covering of these epidermal outgrowths is, as might be expected, much more dense on the sun leaves.

Probably the work of all kinds done by the sun leaves is far greater than that done by shade leaves of the same species. This is partly due to the much greater supply of energy daily received by the former from the sun, and it is also due to their more capacious conducting system and greater supply of chloroplasts. The transpiration of a given area of sun leaves is at times tenfold that of the same area of shade leaves (both being placed for the time in full sunlight).

448. Transition of a plant from shade conditions to sun conditions. It is characteristic of many kinds of forest trees that the young seedlings are much more tolerant of dense shade than the adult trees. Sometimes their seeds will hardly germinate at all unless thoroughly shaded, and the young trees for the first few years flourish best in the shade. Afterwards most trees need a good deal of sunlight, but they may live long with a scanty supply of light. The red spruce sometimes lingers on for

FIG. 365. An epiphytic fern (*Platycerium*) on a tree trunk

The more upright leaves next to the trunk of the tree serve to collect moisture and to accumulate a deposit of decaying vegetable matter, while the outer leaves serve as foliage and bear spores. — After Schimper fifty or a hundred years, reaching meantime a diameter of not more than two inches, and then, on getting more light, shoots up into a large and valuable timber tree.[1]

449. Epiphytes. It is even easier for a plant to secure enough sunlight in a forest region by perching itself upon the trunk, branches, or leaves of a tree than by climbing, as our wild grapevines and the great tropical lianas do. There is a large number of such perched plants, or *epiphytes* (meaning upon a plant), particularly in such tropical forests as those of Fig. 39 and Plate XIII. Epiphytic forms occur among many different groups of seed plants and of spore plants, especially lichens. The staghorn fern, shown in Fig. 365, is a good example of an epiphyte. Instances among seed plants are the so-called Florida or Spanish moss (Plate III) and orchids like those in Fig. 13.

450. Water supply of epiphytes. Epiphytes secure their supply of water and dissolved salts in several different ways, some through roots by absorption from the moist bark on which they grow, others by sending roots down until they reach the earth, others by means of a network of aërial roots fully exposed to the air, — as in the orchid just mentioned, — and still others by means of leaves which function as roots. Some species, like the Florida moss, absorb water very rapidly from dew or rains, while others, as the stag-horn fern (Figs. 272, 365), and *Tillandsia bulbosa*, a relative of the Florida moss, hold water in reservoirs at the bases of the leaves, with or without the aid of spongy decaying vegetable matter. From the great vicissitudes in their water supply most epiphytes among seed plants possess xerophytic characteristics.

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[1] See the *Primer of Forestry*, Part I, United States Department of Agriculture, 1899, pp. 33–35.

CHAPTER XXXVII

PLANT FORMATIONS; ZONATION *

451. Plant formations. One of the first things which the young field botanist learns is the fact that *the distribution of plants depends largely on the character of the ground they occupy.* There is in any small territory, such as a county, for example, one assemblage of plants for the waters of ponds and another for their shores, one for swamps, one for moderately dry uplands, one for very dry hilltops, and so on. The aquatic plants of the sea are very different from those of fresh water. Sandstone and limestone soils have vegetations peculiar to themselves;[1] the long-leaved pine, the scrub pine, and the chestnut are characteristic trees of sandy soils, while most of the oaks, the hackberries, and the black walnut are generally found in limestone regions.

The collection of plants as found in any given kind of station or habitat, especially when prominent and well defined, is called a *formation.* Thus we have marine aquatic formations, sea-beach formations, pond formations, bog formations, sand-hill formations, meadow formations, heath formations, forest formations, and many others such as the student may designate for himself.

452. Plant associations. Usually the plant formation is divisible into assemblages or unit groups, which are much more alike in their vegetation than is the formation as a whole. Thus a woodland formation may consist of pine patches, oak patches, and

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* To the Instructor: If it is necessary to cut down the discussion of these topics to little more than definitions, only the first three sections of the chapter need be read.

[1] Perhaps this is sometimes due to physical rather than to chemical causes. In other words, the chemical differences in soils are usually accompanied by differences in their porosity, their capacity for retaining water, for absorbing heat from the sun's rays, and so on, which greatly modify their effect on plants.

birch patches. A grass-land formation may consist of patches of timothy and others of redtop, and so on. Such minor groups are often called *associations*.

In some cases it may be possible to show that the association is based on the mutual relations to each other of the plants which compose it, while the formation as a whole depends on the characteristics of the station in which it exists, i.e. on soil, climate, and so on.[1]

453. Zonation. The most striking occurrence of plant formations is in localities where sharply contrasted conditions of life exist side by side. It is often possible, within the radius of a few hundred feet, to travel from the floating aquatic vegetation of the deeper waters of a pond, through the rooted aquatic forms of the shallower water, to the sub-aquatic species of the wet shore, then past the sand-loving plants of the sand dunes farther back from the water, and finally into the wood or meadow vegetation of ordinary soil. Such a series of zones is shown in Fig. 366 and in Plate X.

Similar diagrams may be made to illustrate the distribution of plants about a salt spring or pool, along the seashore or the margin of a salt marsh, on the top and sides of an isolated hill with a dry, ledgy, or sandy summit, or even about an old unused gravel pit or a railroad embankment. Less clearly defined but very interesting and extensive zones may be studied with relation to submerged aquatics, particularly among marine plants, as shown in Fig. 202.

Among the most striking and symmetrical instances of zonation are those to be found about the salt marshes of some of the deserts of the far West. The waters of these marshes are too salt to support vegetation, but encircling their borders may sometimes be found as many as six broad concentric bands of abundant vegetation.

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[1] Some authors use the term *association* as an equivalent for the term *formation* as here employed. *Consocies* is sometimes used with the same meaning as is here given to association.

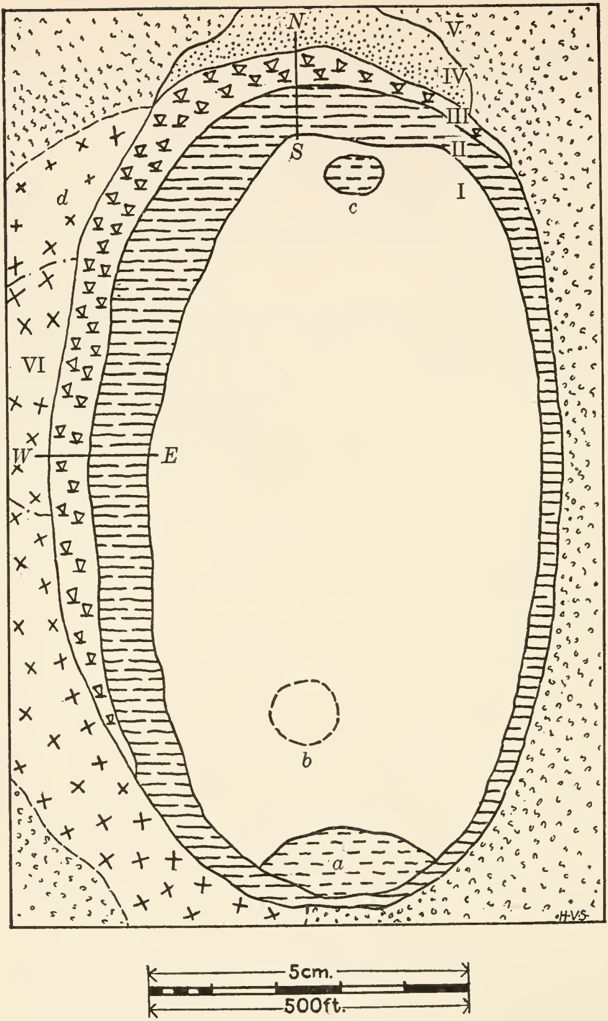

Fig. 366. Zonation about a pond

I, pond; II, bog zone; III, swampy thicket zone; IV, incomplete zone in arid soil of a sand pit; V, dry meadow zone; VI, dry woodland zone; *a*, floating mass of *Eriocaulon*; *b*, deepest area in pond, six to ten feet; *c*, association of tall rushes (*Juncus militaris*); *d*, birch woodland (*Betula populifolia*); *WE*, line intersecting formations of west side of pond; *SN*, line intersecting formations of north end of pond

454. Zonation in Fig. 366. The diagram represents some of the principal formations observed in and about a rather shallow pond in eastern Massachusetts in October, 1905.

The pond was almost encircled by six zones of vegetation, only one of which (the bog zone) entirely surrounded the water. All the zones except that of the meadow consisted of wild species, growing under nearly natural conditions.

The pond itself had a rather scanty algal vegetation, among which the most noticeable forms were a green alga (*Bulbochæte*), related to *Œdogonium*, and a blue-green alga (*Cœlosphærium*).

Seed plants were well represented in the waters of the pond. In the deepest portion, at *b*, no seed plants were found extending to the surface, but there were many young specimens of a rush (*Juncus militaris*) with filiform leaves deeply submerged. In general the pond was populated by pond lilies (*Nymphæa*), cow lilies (*Nuphar*), three or more species of pondweed (*Potamogeton*), with much pipewort (*Eriocaulon*) and duckweed (*Lemna*). In the shallowest portions, usually in six inches or less of water, were found some six other herbaceous species.

The spermatophytic vegetation of the pond may be divided according to its mode of growth into classes as follows:

Floating plants	*Lemna*
Plants which grow rooted and submerged	*Potamogeton*
Plants which grow rooted, but with more or less of the stem or leaf surface in air	*Juncus* *Pontederia* *Nymphæa* *Nuphar*
Plants of shallow water (six inches or less), or which grow on floating rafts like that at *a*, with most of the plant body aërial	*Eleocharis* *Xyris*, etc.

455. Contents of the zones. It would involve too much detail to enumerate the species of the several land zones (II–VI), but they may be briefly summarized as follows:

The bog zone contained some twenty-one conspicuous species, especially peat moss and herbaceous seed plants.

The swampy thicket zone contained mostly shrubs and small trees, including an alder, a blueberry, a pepper bush (*Clethra*), gray birch, and red maple.

The arid soil zone contained more than twenty species, mostly sand-frequenting annual seed plants.

The meadow was growing under artificial conditions, and it was merely noted that its flora consisted mainly of cultivated grasses.

The dry woodland zone contained some twenty-three conspicuous forms. The three principal trees, in the order of their numbers (omitting the region *d*), were white pine, northern pitch pine, and red oak. The forest floor contained an abundant growth of shrubs and herbs. At least five species of the latter were common to the woodland zone and the arid sand zone.

The marked differences in the character of the vegetation of the several zones were almost wholly due to differences in the amount of water supply. Not only would the trees have died if transplanted into the pond, or the pond aquatics have died if removed to the dry sandy soil of the woodland, but in general each set of plants was better off in its own zone than it would have been in any other. The sand-pit flora was, however, only a short-lived succession, soon to be followed by the woodland flora.

456. Similar vegetation due to similar conditions. As soon as one begins to collect plants in a set of localities new to him, he often discovers that his old acquaintances are still to be found grouped as he has been accustomed to see them. The muddy borders of ponds from Maine to Minnesota and beyond are fringed with the same kinds of bur reeds and sedges, set with water plantain and decorated with the soft white blossoms of the arrowhead. The sand dunes along the northern Atlantic coast and those that border Lake Michigan are clothed with a sparse vegetation, which in both cases includes the little beach plum, such coarse grasses as that shown in Plate I, and the straggling sea rocket. Barnyards and waste grounds about farm

Plate X. Zonation about an Ohio pond, showing in all seven zones

After J. H. Schaffner

buildings from Massachusetts to Missouri contain such weeds as the dog fennel, the low mallow ("cheeses"), motherwort, catnip, and some smartweeds.

A little study of such cases soon leads one to the conclusion that these plant associations and multitudes of others exist *because all the plants in each association are adapted to their special environment.* Wherever such an environment occurs such an association will be found in it,[1] or, if not already there, will flourish when introduced.

457. Similar species replace each other. Two sets of localities alike in many respects but unlike in some points are often inhabited by different species of the same genus. For instance, the pine barrens of New England and the adjacent states are commonly covered with the northern pitch pine,[2] while far southward, in sandy soil, its place is taken by the long-leaved pine.[3] Along streams and swamps northward the speckled alder[4] is generally found, while southward the smooth alder[5] is most common. In rich woods of the northeastern United States the painted trillium[6] and the erect trillium ("Benjamin," or "squaw root")[7] are the commonest species, while farther south, in similar localities, the sessile trillium,[8] Underwood's trillium,[9] and the large-flowered trillium[10] are abundant.

In all such cases — and they are very numerous — we are to infer that the genus is peculiarly well adapted to some special set of conditions, as sandy soil, brooksides, or the rich, shaded soil of woodlands. The more northerly species are capable of enduring the severe winters and brief summers of their region, while the more southerly ones perhaps cannot do so. The relative warmth of the climates in which they live may not be the only reason, or even the principal reason, for the

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[1] That is, in localities not separated by such natural barriers as seas, high mountains, or deserts.

[2] *Pinus rigida.*

[3] *P. palustris.*

[4] *Alnus incana.*

[5] *A. serrulata.*

[6] *Trillium erythrocarpum.*

[7] *T. erectum.*

[8] *T. sessile.*

[9] *T. Underwoodii.*

[10] *T. grandiflorum.*

distribution of such plants as those just mentioned, but it is one factor, at any rate, and it is certain that, on the whole, most of our native and thoroughly naturalized plants are growing under what is, for them, the best environment, since they cannot usually be made to exchange places with one another. If a square mile of land in Louisiana were to be planted with Minnesota species, and a square mile in Minnesota with Louisiana species, it is very improbable that either tract, if left to itself, would long retain its artificial flora. To this rule there are, however, important exceptions.

458. Formations of few species. It is not uncommon to find tracts of land or water inhabited by great numbers of seed plants of the same species, so as almost to exclude all other vegetation except microscopic spore plants. Ponds and slowly flowing streams are often filled in this way with the water hyacinth,[1] the water cress, or the American lotus.[2] The canebrakes of the South and the wild rice swamps along northern lakes and rivers are other examples of an extremely simple flora spread over large areas. Prairies not infrequently for many square miles are covered mainly (not entirely) with a very few kinds of grasses. The arid plains of the Rocky Mountain region, over thousands of square miles, contain little vegetation except sagebrush (*Artemisia tridentata*), and immense tracts of snow in the arctic regions are destitute of plant life except for the red-snow alga (*Sphærella nivalis*, Sec. 215), by which they are colored pink.

In all such cases it is evident that the single species or the few species which populate the area can endure the conditions of existence there so well that other plants which migrate into their territory cannot compete with them.

[1] *Eichhornia.*

[2] *Nelumbo.*

CHAPTER XXXVIII

PLANT GEOGRAPHY *

459. Regions of vegetation. The earth's surface (that of the land) has been described by one of the greatest of geographical botanists[1] as divided into twenty-four regions of vegetation. His grouping takes account of all the principal continental areas which have a characteristic set of plants of their own, as well as of the most important islands. But a simpler arrangement is to consider the plant life of the earth as distributed among the following regions:

1. The tropical region.
2. The temperate regions.
3. The arctic regions.
4. Mountain heights.
5. Bodies of water.

Any good geography gives some account of at least the land vegetation of the earth. It is only necessary in the present chapter to point out a few of the most important characteristics of the plants of the areas mentioned above and to give some reasons why the plant population of each has its special characteristics.

460. Tropical vegetation. Within the tropics two of the great factors of plant life and growth, namely, light and heat, are found in a higher degree than elsewhere on the earth. Moisture, the third requisite, is in some regions very abundant (over forty feet of rainfall in a year), or sometimes, in desert areas, almost lacking. We find here, accordingly, the greatest extremes in amount of vegetation, from the bare sands or rocks of the Sahara desert (Fig. 367) to the densely wooded basin of

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* To the Instructor: Unless the present chapter can be discussed in considerable detail, it might better be omitted than hastily dealt with.

[1] A. Grisebach, in *Die Vegetation der Erde*.

the Kongo and of the Amazon. The rainy forests of the tropics contain extraordinary numbers of species. For example, near Lagoa Santa in Brazil, in an area of three square miles, there are found about four hundred species of trees. Xerophytic plants, many of them with extremely complete adaptations for supporting life for long periods without water, are characteristic of tropical deserts, while many of the most decided hydrophytes among land plants are found in the dripping sub-tropical forest interiors. Throughout a large part of the belt, reaching five degrees each way from the equator, there are daily rains the year round.

FIG. 367. Hills of drifted sand in the Sahara

After W. M. Davis

461. Vegetation of temperate regions. We are all familiar in a general way with the nature of the plant life of the north temperate zone; that of the south temperate is in most ways similar to our own. Most of the annuals and biennials are of a medium type, not decided xerophytes nor hydrophytes, and the perennials are mainly tropophytes. There are no desert areas so large or so nearly destitute of plants as those found in sub-tropical regions, neither are there any such luxuriant growths as occur in the rainy forest regions of the tropics. On the other hand, the largest trees on earth, the giant redwoods, or *Sequoias* (Fig. 33), occur in the temperate portion of North America, along the Sierra Nevada, and the taller, though less bulky, gum trees (*Eucalyptus*) of Australia grow in a warm temperate region.

462. Temperate plant associations due to special conditions of soil. Even where the climate is a moderate one as regards temperature and rainfall, peculiar soils may cause the assemblage of exceptional plant associations. Some of the most notable of such associations in temperate North America are those of the salt marshes, the sand dunes, and the peat bogs.

In salt marshes the water supply is abundant, but plants do not readily absorb salt water by their roots, so that the plants which grow in salt marshes usually have something of the structure and appearance of xerophytes. Some of them are fleshy (Fig. 368), and some species are practically leafless.

Sand dunes, whether along the seacoast or near the Great Lakes, offer a scanty water supply to the roots during much of the year, and the soil water contains less of the raw materials for plant food than is offered by that of ordinary soils. Many grasses thrive, however, in these shifting sands (Plate I), and some, like the beach grass (*Ammophila*) of the Atlantic coast and the Great Lakes, will continue to grow upward as the sand is piled about them by the winds, until they have risen to a level of a hundred feet above the starting point.

FIG. 368. A halophyte (*Salicornia*)

The water of peat bogs contains little mineral matter, and only a very scanty supply of nitrogen, in the form of nitrates dissolved in it. The bog plants, therefore, must either get on with an exceptionally small supply of nitrogen, or they must get it from an unusual source. The peat mosses adopt the former alternative, while the sundews, the pitcher plants, and some other species adopt the latter and derive their nitrogen supply largely from insects which they catch, kill, and digest.

463. Arctic vegetation. The seed plants of the arctic flora are mostly perennials, never trees, though many of the species, as the willow, alder, and birch, belong to groups that are trees in other regions. By the large bulk of the underground portion as compared with that of the part above ground, they are adapted to a climate in which they must lie dormant for not less than nine months of the year. The flowers are often showy and appear very quickly after the brief summer begins. Mosses and lichens are abundant, — the latter of economical importance because they furnish a considerable part of the food of reindeer.

Fig. 369. A plant of arctic willow

About natural size

464. Mountain or alpine vegetation. In a general way the effect of ascending a mountain, so far as vegetation is concerned, is like that of traveling into colder regions. It was long ago suggested in regard to Mount Ararat, that on ascending it one traversed first an Armenian, then a south European, then a French, then a Scandinavian, and finally an arctic flora. Up to a certain height, which varies in different latitudes, the slopes of mountains are very commonly forest-covered. The altitude up to which trees can grow, or as it is commonly called in this country the "timber line," is somewhat over twelve thousand feet in the equatorial Andes, and lessens in higher latitudes as one goes either way from the equator, until in the arctic regions it reaches sea level. In the White Mountains, for instance, the timber line only rises to about forty-five hundred feet. The seed plants of alpine regions in all parts of the earth have a peculiar and characteristic appearance. It is easiest to show how such plants differ from those of the same species as they look when growing in ordinary situations by reference to the plants themselves or to good pictures of them (see Fig. 372). The differences between alpine and non-alpine plants of the same or closely related species have been summed up as follows[1]: "The alpine individuals have shorter stems, smaller leaves, more strongly developed roots, equally large or somewhat larger and usually somewhat more deeply colored flowers, and their whole structure is drought-loving (xerophilous)."

FIG. 370. Trees near the timber line on the slope of Pikes Peak

After W. M. Davis

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[1] By A. F. W. Schimper.

Trees at great elevations are stunted and gnarled by scanty nutrition and pressure of wind and snow (Fig. 370).

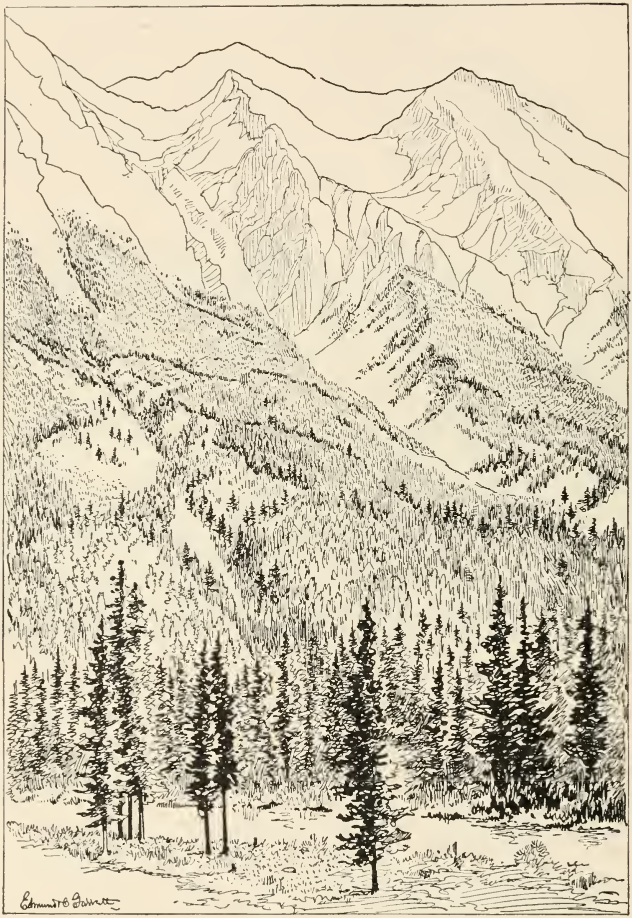

Fig. 371. Decrease in size of trees at high elevations (Canadian Rockies)

Where the prevailing winds come mainly from one quarter, all the trees of considerable areas may be inclined strongly in one direction, as in Plate XI.[1]

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[1] This phenomenon is also very noticeable along many coasts.

Plate XI. Trees on Pikes Peak, leaning from constant mountain winds

After F. E. Clements

The gradual diminution of the height of the trees on ascending a mountain is well shown in Fig. 371.[1] The treeless character of the mountain summit is also plain.

Recent experiments have shown that many ordinary plants promptly take on alpine characteristics when they are transferred to moderate heights on mountains. For instance, a rather commonly cultivated sunflower,[2] when planted at a height of about sixty-five hundred feet, instead of having a tall, leafy stem, produces a rosette of very hairy leaves lying close to the ground, thus becoming almost unrecognizable as a sunflower. The change is even greater than that shown in the rock rose (Fig. 372) cultivated by the same experimenter. The peculiarities of alpine plants appear to be due mainly to the intense light which they receive during the daytime,[3] to the strongly drying character of the air in which they grow (due partly to its rarefaction), and to the low temperature which they must endure at night.

Fig. 372. Two plants of rock rose (*Helianthemum*) *A*, low ground form; *B*, alpine form. Both drawn to the same scale

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[1] Part of the diminution is only apparent, — the effect of distance, — but the growth at the highest levels is often less than waist high.

[2] *Helianthus tuberosus*, the so-called Jerusalem artichoke.

[3] The experiments of Professor Frederic E. Clements on Pikes Peak, however, seem to show that light is not a principal factor in the production of alpine characteristics in plants.

465. Aquatic vegetation. Plants which live wholly in water often need a less complicated system of organs than land plants. True roots may be dispensed with altogether, as in many seaweeds, in most fresh-water algæ, and in some seed plants. Many such plants have mere holdfasts that keep them from being washed out of place. In the duckweeds (Fig. 355) the roots answer the purpose of a keel and keep the flat expanded part of the plant from turning bottom up. The tissues that serve to strengthen the plant body are not much developed in submerged aquatics, since the water supports most, if not all, of the weight of the plant. Stomata are absent, and the absorption of carbon dioxide and giving off of oxygen go on directly through the delicate cell walls, unprotected by an epidermis (Fig. 354, *B*). Submerged aquatic seed plants occur in considerable abundance in sea water as well as in fresh waters, but the marine forms do not include many species.

466. Influence of rainfall in determining regions of vegetation. While the mean annual temperature and the extremes of heat and cold, humidity of the air, force and direction of winds, elevation above sea level, and nature of the soil are all factors in determining the boundaries of regions of vegetation, there is no factor more important than the annual rainfall. Of course the rainfall itself is largely determined by several of the other circumstances above mentioned.

In the United States this varies greatly, the yearly averages for some of the most important areas being about as follows:

AVERAGE RAINFALL PER YEAR

REGION	INCHES
New England and Middle States	43
Eastern Gulf States	55
Ohio basin	44
Missouri basin	31
Rocky Mountains, middle of eastern slope	20
Rocky Mountains plateau, middle	9
Pacific slope, northern portion	37
Pacific slope, southern portion	10

It is evident that the rainfall increases southward along the Atlantic coast, but that on the Pacific coast it diminishes southward. Passing from either coast inland, one finds the rainfall diminishing until it reaches a minimum in the Rocky Mountain region.

467. Plant geography of the United States. All of the continuous territory of the United States[1] lies in the north temperate zone. There is material for volumes in the discussion of the distribution of plants over our territory in this continent alone, but it is possible to sum up a brief outline of the matter in a few pages. Excluding the floras of many single mountains and mountain ranges, the land surface of the country may for botanical purposes be divided into four great areas, as follows:

FIG. 373. Annual rainfall of the United States

Darkest shade, over 80 inches; lighter vertical lines, from 40 inches to 80 inches; horizontal lines, from 20 inches to 40 inches; blank, from 10 inches to 20 inches; dotted, less than 10 inches. — After W. M. Davis

The forest region. This occupies the eastern and central portion of the United States. It is bounded on the west by an

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[1] That is, not counting in Alaska, our West Indian possessions, the Hawaiian Islands, or the Philippines.

irregular line, most of which is east of the hundredth meridian. In some places this forest boundary lies considerably east of the Mississippi River, while in others it extends from the river five hundred miles or more to the westward.

The plains region. This stretches westward from the region above-named to the Rocky Mountain plateau.

The Rocky Mountain region. This includes the Rocky Mountains, the Sierra Nevada, and the various plateaus between them.

The Pacific slope. This extends from the Cascade Range and the Sierra Nevada to the sea.

468. The forest region. The forest region is mainly remarkable for its great variety of hardwood trees, of which it contains a larger number of useful species than any equal area of the earth with a temperate climate. Perhaps the most important of these are the oaks; but other genera, such as the hickory, the tulip tree, and the sassafras, are more characteristically American. In the northeasterly portion there are extensive forests of the cone-bearing evergreens, such as pines, spruces, hemlocks, and cedars; the other trees which accompany these are mostly deciduous hardwood species. In the southerly portion the forests are partly of coniferous evergreens (Fig. 392) and partly of deciduous mesophytes, such as hickories, beeches, oaks, elms, hackberries, magnolias, and sycamores. There is also a considerable admixture of such hydrophytes as the water hickory, the sweet bay (*Magnolia*), the anise tree (*Illicium*), the custard apple (*Anona*), the red bay (*Persea*), the loblolly bay (*Gordonia*), and the sour gum (*Nyssa*), due to the mild, moist climate.

This region was never completely forest-covered. Areas of prairie, so-called "openings" in the hardwood forests (Fig. 393), extensive marshes, and some heaths have for ages been treeless, or nearly so. Generally, in the older states, the land most desirable for cultivation has been tilled so long that it is difficult to find portions in anything like their primitive condition. It is only in broken country like that of the mountainous regions

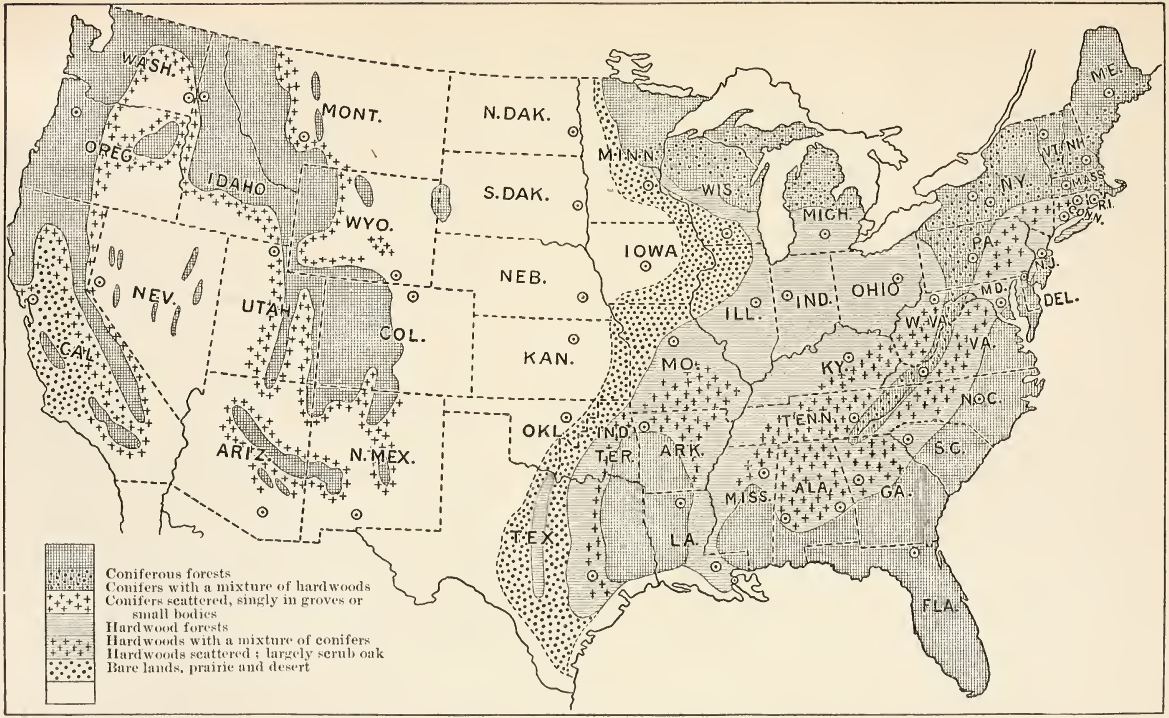

FIG. 374. General forest map of the United States

After Roth, *First Book of Forestry*

of eastern Tennessee and North Carolina, the Adirondacks and the White Mountains, in swampy river valleys, in a few great marshes, or in sterile, sandy pine barrens, that one can find the original flora in its natural condition.

Comparing our forest region with the parts of Europe which resemble it most in soil and climate, our flora differs notably in possessing such leguminous trees as the locust and the honey locusts, in the abundance of members of the heath family, and in wealth of Composites, especially asters and golden-rods.

In very many instances our eastern flora when it differs most notably from that of Europe greatly resembles that of China and Japan. This is undoubtedly due to the fact that these American species and kindred Chinese and Japanese ones had in an earlier geological age a common ancestry.

On account of the great length of the territory along a north and south axis and the diversified nature of its surface, the flora of the forest region varies from a sub-tropical one in southern Florida to one with a plentiful sprinkling of sub-arctic species along portions of the northern border, particularly on the higher mountains.

469. The plains region. This region rises with a gradual ascent from the prairies (some of which occur from Ohio westward and over great areas border the west bank of the Mississippi), until an elevation of five thousand feet or more is attained, when the plains reach the Rocky Mountain system. There is no sharply defined line of demarcation between the prairies of western Kansas, western Iowa, Minnesota, Nebraska, and South Dakota, with less than 20 per cent of the surface wooded, and the high plains, wholly treeless except along the streams (Plate IX, upper figure), that flank the eastern border of the Rocky Mountains. The lack of trees in the prairie and plains region has been attributed to various causes, but the principal ones are doubtless forest fires, the scanty rainfall, and the occurrence in winter of severe drying winds, at a time when the roots can draw no moisture from the frozen soil.

The vegetation of the prairies consists primarily of a considerable number of vigorous sod-forming grasses intermixed with many other seed plants. Notable among these are several species of the pea family, many golden-rods and asters, and some larger Composites, such as sunflowers and rosinweeds (*Silphium*). Especially striking is the display in late summer and autumn of many showy Composites, such as the blazing star (*Liatris*), the cone flower (*Rudbeckia*), and the tickseed (*Coreopsis*).

The vegetation of the high treeless plains is, in the eastern portion (Plate IX, lower figure), characterized mainly by the close mats of the short, xerophytic buffalo grasses and grama grasses of a grayish-green color. Among these grasses are scattered prickly pear cactuses (*Opuntia*), milkweeds (*Asclepias*), and thistles. After the drying up of the grasses in early July, there is sometimes hardly any living vegetation left above ground except that of the cactuses.

Toward the Rocky Mountains, as the soil becomes more alkaline, various species of wormwood or sagebrush, and members of the pigweed family (*Chenopodiaceæ*) become predominant. The universal sagebrush (*Artemisia tridentata*) plainly shows its xerophytic character by its deep-reaching roots, its reduced leaf area, and its strongly hairy surface.

470. The Rocky Mountain region. The Rocky Mountain region includes a very great variety of plant formations, from the heavily wooded mountain slopes and valleys to high sterile plains which are almost deserts. Cone-bearing evergreen trees, especially the true spruces, the "Douglas spruce" (*Pseudotsuga*), and several pines, are very characteristic of the forests (Plate XII). Great numbers of alpine species of herbs and shrubs are found on the mountains at and above the timber line. In the "alkali" regions, where the soil is too full of mineral salts to permit ordinary plants to grow, many kinds of halophytes, such as the salty sage (*Atriplex*), the greasewood (*Sarcobatus*), *Salicornia*, and *Suæda*, occur.

Most notable among the saline areas is the Great Basin, west of the Great Salt Lake, a dreary region in general, destitute of natural grass lands or trees, but with a scattered vegetation of low gray or dull-green shrubs and herbs. In the lower highly alkaline valleys are found such halophytic species as those above-named, while the drier valleys and foothills are somewhat evenly covered with sagebrush.

In the South, cactuses, palms, and tree yuccas abound. Wherever the soil is gravelly throughout the southern arid region, up to an elevation of five thousand feet or somewhat more, the creosote bush (*Larrea tridentata*) is often as exclusive in its occupancy of the ground as the sagebrush is in the central and northern parts of the Great Basin.

Here are some of the most notable arid regions of the United States, such as the Mohave Desert, the Ralston Desert, and the Colorado Desert of southern California. The intense dryness of such areas may be understood from the fact that the average rainfall of ten of these deserts is only five inches a year, and the temperature in one of them (at Fort Yuma, Arizona) remains for weeks as high as 118° during the day, with sometimes only a little over one half inch of rain a year.

471. The Pacific slope. The Pacific coast region offers far less marked contrasts between the summer and winter temperature than are found along the Atlantic coast.

On the other hand, there is, in the southern portion of the region, a sharply defined division of the year into a dry and a rainy season. At San Diego the dry season begins with April and lasts for seven months. The development of vegetation, therefore, as in the northerly part of the plains region east of the Rocky Mountains, is most rapid in spring and largely ceases when the soil has become parched by the summer's heat.

The flora of the Pacific slope is best known by its extraordinary coniferous evergreen trees. In the moss-carpeted woods of the northern portion (bounded on the south by the forty-first parallel) are found the Port Orford cedar (*Cupressus Lawsoniana*),

Plate XII. A coniferous forest in central Colorado, Douglas spruce (*Pseudotsuga mucronata*)

After F. E. Clements

the red cedar, the tide-land spruce (*Picea sitchensis*), and the hemlock spruce (*Tsuga heterophylla*). In places there occur dense thickets of hazel and maple, or of shrubs of the heath family.

In the southern portion of the Pacific slope (from the forty-first to the thirty-fifth parallel) are found the well-known California evergreen conifers, such as the sugar pine (*P. Lambertiana*) of the coast, the yellow pine (*P. ponderosa*), and in the mountains the smaller redwood (*Sequoia sempervirens*) and the giant redwood (*S. gigantea*, Fig. 33), the largest and by far the most monumental of trees.

Among the characteristic features of the California flora is the abundance of xerophytic shrubs and small trees, many of them broad-leaved (not coniferous) evergreens, forming the chaparral thickets. Among these are members of the oak, the rose, the sumach, the heath, the buckthorn, the composite family, and many others.

In southern California, on account of the long dry season, plants with large roots or rootstocks, and bulb-bearing plants, many of them belonging to the lily family, are abundant.

In the deserts and on their borders are numerous cactuses and other succulent forms. Among the most characteristic desert plants are the Spanish bayonets, or *Yuccas*, some of them tree-like in form and size.

CHAPTER XXXIX

VARIATION, MUTATION, AND ORIGIN OF SPECIES

472. Variations of plants. One of the foundation principles of scientific farming and gardening is that seeds will grow into plants like those which produced them. Not only is it assumed that grains of corn will grow into corn plants and beans into bean plants, but also that any special variety of sweet corn will produce its like, yellow-eyed beans their like, and so with multitudes of familiar cases. Closer observation, however, shows that no two of the hundreds or thousands of plants raised from the seeds of a single parent plant will be exactly like each other or the parent. Generally the variations are very slight, and most of them fail to continue themselves in succeeding generations so as to establish new varieties of plants.

473. Variations in one direction. While variation generally goes on in all directions, so that one of a brood sprung from a given parent will be smaller and another larger, one more and another less hairy than the parent plant, and so on, it is not uncommon to find what may be called *definite variation,* in which the changes all lead toward a definite new type. The behavior of lowland forms planted in alpine regions (Sec. 464) is a good instance of the kind. It is well known, too, that seed from northern localities when planted farther south will produce earlier crops than can be obtained from southern seed. American varieties of onion, after being grown for a series of years in England, become habituated to the longer mild season there, and when the seed is brought back to America the plants grown from it fail to mature their bulbs before the coming of the frost.

Such facts as these seem to indicate that characteristics which have been impressed upon the plant by external influences, such as those of soil and climate, may be transmitted to its descendants. If it be so, then the origination of new forms of plants by the inheritance of such characteristics must be extremely common.

474. Mutations of plants. Much attention has lately been given to the occurrence among plants of seedlings which differ in a marked way from the parents. It would involve too much detail to describe the exact nature of the differences between the seedlings of the evening primrose,[1] which has been most studied in this connection, and its offspring, but they are as great as those between an apple tree and a pear tree. Such abrupt and extensive changes are called *mutations.* A few of the most important facts so far known in regard to mutation are:

1. New species[2] appear suddenly among the offspring of the parent form.
2. The individuals of the new species constitute only a small per cent of any given brood.
3. The new species reproduce themselves accurately, showing no decided tendency to return to the parent form.

475. Importance of adaptiveness in plants. It may be inferred from Chapters XXXI and XXXIV that a premium is set on all changes in structure or habits which may enable plants to resist their living enemies or to live amid partially adverse surroundings of soil or climate. It would take a volume to state, even in a very simple way, the conclusions which naturalists have drawn from this fact of a savage competition going on among living things, and it will be enough to say here that *the existing kinds of plants to a great degree owe their structure and habits to the operation of the struggle for existence,* together with their *response by means of variation to changes in the conditions by which they are surrounded.* How the struggle for existence has brought about such far-reaching results will be briefly indicated in the next section.

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[1] *Œnothera lamarckiana.*

[2] For a definition of the term *species*, see Sec. 189.

476. Survival of the fittest. A change in the characteristics of a species may have no effect on its ability to contend with a hostile soil or climate, with parasitic plants or destructive insects or other animal foes; but often alterations in the structure or the habits of a plant may give it a considerable advantage over its unchanged neighbors. For instance, a decided increase in hairiness would tend to protect the plant from damage by long droughts, and also (in countries where snails destroy much vegetation) from having its leaves eaten. Nuts with harder shells would escape being destroyed when the ordinary ones would be cracked and eaten by wild animals. Red berries of the European holly are carried off by birds more extensively than yellow ones, and thus the undigested seeds of the former variety are more widely sown.

In meadows which are mown once a year, only those plants can surely reproduce themselves by seed which ripen their seeds either before or after the time when the grass is cut. Individuals which can do this stand a vastly greater chance of perpetuating themselves than do those which are cut down just before their seeds have matured. For this reason certain kinds of meadow-frequenting plants[1] have developed early-blooming and late-blooming forms, which would probably never have become abundant in regions where the grass was not mown.

Whatever the nature of the advantages given to one form or set of forms over another in the competition which always goes on under natural conditions, it results in what is sometimes called *survival of the fittest*, and sometimes *natural selection.*

477. Have species arisen by variation or by mutation? The theory that species (and later genera and higher groups) arise by slow degrees from the operation of natural selection acting on the slight variations which constantly occur among animals and plants was first fully set forth by Charles Darwin in 1858.[2]

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[1] Species of *Gentiana*, *Euphrasia*, and *Rhinanthus*.

[2] Darwin's paper on this subject was the result of over twenty years of study, and was read by him to accompany a paper containing similar views which had been sent from the East Indies by Alfred Russel Wallace.

The theory that species spring suddenly from mutations was advanced by Professor Hugo de Vries, of Amsterdam, Holland, in a work on the mutation theory, published in 1901 and 1903.

Botanists at present are considerably divided on the question of the origin of species, some believing that they are mainly derived from the perpetuation and intensification of slight variations, while mutations are so infrequent as not to signify much in this connection; others, again, believe that mutations are the source of species, and that variations can only give rise to varieties. There seems to be no good reason for doubting that both variation and mutation have been and are efficient in the production of new species.

CHAPTER XL

PLANT BREEDING

478. Definition of plant breeding. The selection and maintenance of the most desirable varieties of cultivated plants must, to some extent, have occupied the attention of agriculturists during all the thousands of years since farming began.[1] From the writings of Virgil and other Latin authors it is clear that Roman farmers practiced careful selection of cereals for seed, knowing that without this their crops would diminish. But it is only within a short period that scientific principles have been brought to bear on the process. In fact, it is stated that the systematic improvement of races of cultivated plants began in the middle of the nineteenth century. The intentional production and perpetuation of new varieties is known as *plant breeding.* It is based upon the methods outlined in Secs. 479 and 480.

479. Single selection and continued selection. New varieties of plants, whether wild or cultivated, are constantly being produced by ordinary variation and by mutation (Secs. 472–474). In a single field, supposed to contain only one kind of wheat, a trained botanist once found twenty-three well-marked varieties, one of which became the parent of a sort that has remained famous for over three quarters of a century. The plant breeder is constantly on the watch for promising varieties, preserving all which seem likely to be of use. While it is a slow, uncertain method to await the appearance of variations in any desired direction, and then to rely on the perpetuation of these, the large number of valuable new varieties thus secured warrants all growers

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[1] In China the cultivation of rice, wheat, two kinds of millet, and soy beans dates back at least 4600 years.

in being on the lookout for variations which promise new values. The surer plan is to take seed from a considerable number of parent individuals which possess the desired quality in a high degree, raise plants from each of these, discard plants of this second generation from all parents whose progeny does not excel, and continue selecting from these superior stocks. In this way many characteristics, such as abundant yield, hardiness, early ripening, whiteness in the case of flour, increased percentage of sugar in sugar beets, or improved size or flavor in tomatoes may be secured in a few years of careful breeding. This may be called the selection of good parent plants.

480. Production of hybrids. An important method of making new varieties is by *crossing*, or *hybridizing*, — that is, by pollinating the pistil of one species or variety with pollen from another species or variety. The offspring of cross pollination is known as a *hybrid*.

The process of crossing two species is comparatively easy. If plum blossoms, for example, are to be hybridized, the operator must gather enough of those from which pollen is to be collected, brush or shake off the pollen, and, if necessary, keep it in a cool place until needed.[1] Most of the flower buds are removed from the tree the flowers of which are to be pollinated, and just before the opening of those buds which are left the corolla, with its attached anthers, is cut away, as shown in Fig. 375, and pollen applied to the stigmas with a camel's-hair pencil or, better, with the finger tip. If fertilization results, and plums with good seeds are produced, they must be planted, and seedling trees grown from them. These might be allowed to grow until they blossomed, but years of valuable time can be saved by grafting the young seedlings upon other plum trees. When blossoms of the hybrid form are secured, some of them may be fertilized with pollen of either of the parent species,

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[1] Some kinds of pollen, as that of the pansy and the peony, are said to remain good for weeks, and that of the date palm for more than a year; but in general, pollen should be used as soon as possible.

and others with pollen of different species of plum. All of the seeds obtained from the various crosses should be planted, and the seedlings which are produced by them should be examined, and retained or destroyed according to their apparent value. To the experienced plant breeder the appearance of the seedling trees, long before they are old enough to blossom, indicates so much as to the nature of their fruit that many varieties can be discarded as soon as the young plants have developed well-grown shoots. The distinctive work of hybridizing is to secure parent plants better than any which exist in the foundation species or varieties. The work of choosing a large number of the most promising hybrid plants and of testing their breeding power, so that only the blood, so to speak, of the very best may be retained, is the same as breeding by selection mentioned above. In the occasional hybrid plant, possibly one out of ten thousand, are combined the best in the two parents, or possibly, as some believe, newly created characters may arise.

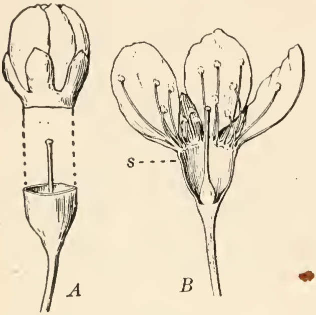

Fig. 375. A plum blossom prepared for hybridizing

A, unopened blossom cut round just below the insertion of the stamens, to remove the latter; *B*, lengthwise section of a fully opened blossom, showing the level *s* at which the cutting should be done

481. Some results in breeding by selection. To give an account of the results of selection as applied to cultivated plants would be to write a history of the variations and improvements in all our ornamental and useful plants under cultivation. In this place it must suffice to give a very few illustrations of the kind and amount of improvement brought about by such selection as is outlined in Sec. 479.

482. Selection among apples. Much of the improvement in apples was brought about before the literature of plant breeding began. It is not certainly known where the cultivated apple originated, but an eatable variety probably occurred in prehistoric times throughout the territory extending from the Caspian Sea nearly to Europe. Small forests of wild apples have been described in modern times, growing near the southeast end of the Black Sea.

The dwellers in pile-built houses in the lakes of northern Italy, Savoy, and Switzerland, several thousands of years ago, laid in stocks of apples cut and dried for winter use. Some of these apples appear to have been cultivated, but they were very small, — inferior in size to any modern variety except some crab apples. How great a gain in the size of apples has been brought about by cultivation and selection may be inferred from Fig. 376. This increase in bulk is accompanied by a decrease in the number of matured fruits in a cluster. Originally several of the flowers developed into apples, but in modern improved varieties usually all but one of the flowers fail, as is shown in the case of the pear (Fig. 83).

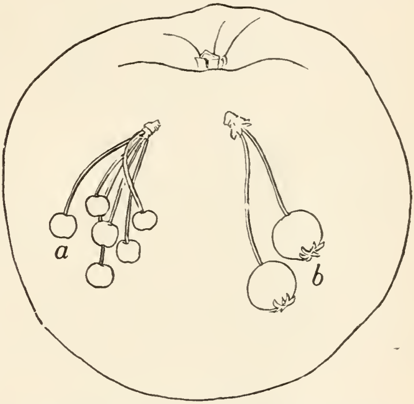

Fig. 376. Effect of cultivation upon the size of apples

The Bismarck apple, with *a*, the wild Asiatic crab apple (*Pyrus baccata*), and *b*, the European wild apple (*P. malus*). All half natural size. — After Hodge

Most of the varieties of apples in our present orchards are descendants of seedlings sprung from trees introduced from western Europe. In the Northwest, where only the hardiest kinds can endure the severe climate, some of the most successful sorts are importations from central Russia, and others are from seedlings of Russian and the hardier American varieties, or from hybrids produced by accident or design.

483. Selection among beans. The common bean (*Phaseolus vulgaris*) is of uncertain origin, but there is a good deal of evidence to show that it came from western South America. Its cultivation in Europe appears to have begun soon after the discovery of America. As is well known, the number of varieties in cultivation is very large, and in few plants is it easier than in beans to produce new varieties by selection.

Bean breeding for the large seedsmen is a skilled industry. It is said that a seedsman may even advertise a new kind of bean under an attractive name before the variety has been produced, then order it of his bean grower, and in the course of two or three years have seed ready for his customers. On the farm of one large bean grower nearly 70 standard varieties are raised for seed on a large scale, and some 200 sorts are being tested to establish their value or to produce new kinds. All possible pains are taken by means of high cultivation to increase the bearing qualities of the plants and also to encourage variation. Every variety, whether a standard one or a novelty, is kept to the desired type by the careful inspection of every plant, those which fall short in any respect being carefully destroyed.

While new kinds are nowadays generally secured by scientific plant breeding, sometimes valuable sorts are obtained from chance seedlings, as in the case of a well-known dwarf Lima bean which sprang from seeds gathered on a Virginia roadside some time before 1885.

484. Selection among corn. Indian corn was cultivated by the ancient Peruvians and the Mexicans. Its original home as a wild plant was probably on or near the west coast of South or Central America. Numerous rather permanent kinds which "come true from the seed" (*races*), such as field corn, sweet corn, and pop corn, have long been known, and some of these races present many varieties.

Scientific corn breeding has been practiced for much less than a generation, but the results already attained are of great practical importance.

Leaving out of account the very extensive use of the stems and leaves of the corn plant for forage, and considering only the value of the grain produced, corn breeding may be carried on to secure, among other less important qualities, the following results:

1. A larger yield per acre.
2. A higher percentage of any one of the three principal constituents of the grain, — starch, proteids, and oil.
3. Early maturing, for growth in the more northerly states.

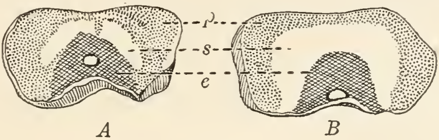

Fig. 377. Kernels of corn with high and with low proteid contents

A, high proteids; *B*, low proteids; *p*, horny layer, consisting largely of proteids; *s*, white starchy portion; *e*, embryo. — After University of Illinois Agricultural Experiment Station, *Bulletin No. 87*

1. *Yield.* The corn crop of the United States is worth about a billion dollars a year for the grain alone. On farms of the

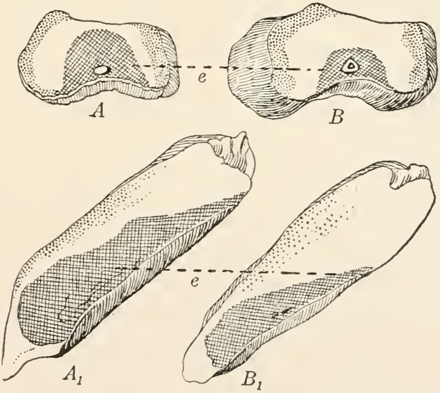

Fig. 378. Kernels of corn with high and with low oil contents

A, A_1, cross and lengthwise section of high oil kernels; *B*, B_1, sections of low oil kernels; *e*, embryo. Most of the oil is contained in the embryo, so that a large embryo means a large percentage of oil. — After University of Illinois Agricultural Experiment Station, *Bulletin No. 87* greatest producing state, Illinois, the average crop is hardly thirty bushels per acre. The use of choice seed has been found to increase the production from 10 to 20 per cent, and it is a moderate estimate which assumes that the universal use of improved seed would add 10 per cent to the total corn crop of the country. This would add over $100,000,000 to the annual receipts of our corn growers.

2. *Improved quality.* In every 100 pounds of ordinary shelled corn there are, in round numbers, about

8 lb. embryo (of which 3 lb. are oil);
13 lb. gluten, or proteids of the endosperm;
64 lb. starch.

There is a demand for a limited amount of corn with a high per cent of oil as a source of corn oil. At the Illinois Agricultural Experiment Station the attempt has been made to breed varieties of corn with high and with low percentages of oil. One variety was secured with nearly 7 per cent and another with less than 2 per cent.

In the same way, that is by means of continued selection, carried through many generations, varieties with much or little starch can be obtained.

3. *Early maturing.* Corn was originally a tropical or subtropical plant, requiring a long growing season. Quickly maturing varieties had, however, been secured by the native races even at the time of the discovery of America by Columbus. At present there are varieties ranging all the way from the eighteen-foot kinds that require a growing period of six months, to the two- or three-foot kinds that mature in ninety days or less.

The most important problem that presents itself to the plant breeder in this connection is that of increasing the yield per acre for each of the agricultural regions where corn is produced, whether in the North, where short-stalked, early-maturing kinds are needed; in the great corn belt; or in the South, East, or West, where varieties are needed which are bred to make the best yield of grain or of fodder, or of grain and fodder combined. This plant is being especially modified for many agricultural regions possessing distinctive soil and climatic conditions, and is more easily adapted to locality than are most plants.

485. Selection among wheat. Wheat of many varieties has been cultivated for thousands of years throughout a territory ranging all the way from China to western Europe. The original home of the plant is not known, but perhaps it was in Mesopotamia, between the Tigris and Euphrates rivers. In Europe systematic attempts to procure improved varieties of wheat by selection date back well toward the beginning of the nineteenth century. Some good varieties were originated in our own country in the early sixties, but more wheat breeding is now done in a single year in the Agricultural Experiment Station of a great wheat-raising state, like Minnesota, than was done in the whole United States prior to 1890.

It will give some idea of the extreme care with which wheat breeding is now conducted to give the barest outline of the mode of procedure in the Minnesota Station.

As a beginning, 10,000 good kernels of some desirable variety of wheat, old or new, are carefully chosen. These grains are planted 4 inches apart (or 5 inches for winter wheat), one seed in a hill, and every plant receives a number. About 95 per cent of the poorer plants are weeded out by hand before harvesting the seed wheat, the heads of the remaining plants are cut off, and those of each plant are preserved in an envelope. After drying, the heads are weighed, and those of all but a few of the best-yielding plants are thrown away.

The second season there are sown in a separate plot in the wheat-breeding nursery about a hundred seeds from each of the plants chosen. Each of these hundred-groups (*centgeners*), sprung from a single mother plant, is given a distinguishing number. When the wheat is mature the relative size and strength of the plants in each plot are noted and recorded, and by separately harvesting and weighing each little plot the breeding power of each parent plant is measured in terms of the average of its progeny. A select head is chosen from each of several of the best plants in every plot, and the seed from these is saved.

A third year and a fourth year hundred-group plots are sown and managed as just described, and at the end of the period the most promising varieties are taken to field trials. Here they are tested, under ordinary farm conditions, in comparison with the wheats commonly grown, and the best, if it stands severe milling tests, is then propagated for distribution, under suitable designating numbers, to wheat growers throughout the state.

The rate at which new varieties can be propagated may be gathered from the history of one of the most famous new wheats, "Minnesota No. 163," a variety bred by selection. This sprang from a single grain planted in 1892. In 1893 the product consisted of 75 plants; in 1894 a small field plot was grown; in 1898 the crop amounted to some 300 bushels of seed wheat, which was distributed among about 50 farmers throughout the state. It is estimated that in 15 years from the time of planting the single original seed the entire wheat crop of Minnesota, covering some 5,300,000 acres, might have been made to consist of this variety, and that it does actually cover millions of acres, adding about two dollars per acre to the value of the crop.

It is not yet possible to state how much can be gained in quality and quantity of wheat production by careful culture and breeding. But it is interesting to note that in a good wheat year (1895), when the average crop per acre on the University of Minnesota farm was 23 bushels, there were 4 improved varieties which yielded over 40 bushels per acre. In 1896, when the average crop for the state was 14.2 bushels per acre, out of 32 improved varieties on the University farm there were 24 varieties which yielded 21 bushels per acre or more, 2 of them yielding 33 bushels. That is, three quarters of the varieties yielded at least $1\frac{1}{2}$ times as much as ordinary wheat on other farms, and 2 varieties yielded about 2$\frac{1}{3}$ times as much. The yield was increased on the farm mentioned both by good farm management and by breeding into the varieties stronger power of yielding.

In 1902 one of the improved wheats, "Minnesota No. 169," was given an extended trial in various parts of Minnesota. It yielded on the average 33 bushels per acre, or 18 per cent more than the ordinary varieties. This variety probably now covers half a million acres, in several states, and yields at least two dollars per acre more value than the varieties (mainly the "blue stem," its parent) which it is rapidly displacing over an area of several million acres devoted to hard spring wheat. The importance of every increase in production is evident when one considers the annual value of our wheat crop, from $250,000,000 to $500,000,000.

486. General results of hybridization. The relative importance of hybridization, and of continued selection alone as means of securing valuable new varieties of cultivated plants, is largely to be worked out in each class of plants. Plant breeding as a science is too new to give material for answering nearly all the questions that naturally arise in regard to how varieties may be most rapidly improved. Hybridizing often brings about great changes in the offspring, and there are increased chances that some of the new forms will be more valuable than any which could be discovered among the foundation varieties. In the case of species perpetuated by grafting, as of certain trees, and plants propagated by roots, rootstocks, or tubers, as potatoes,[1] it is very easy to secure purebred stocks. In plants grown from seed, especially if the species is more or less open-pollinated,[2] there is always a most important question as to how many generations must elapse before the hybrid varieties can be selected "true to seed."

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[1] Varieties among these are called *clonal* varieties (from *clon*, meaning a cutting or scion).

[2] That is, if the flowers are open to cross pollination.

Some of the most important results in variety making by hybridization have recently been obtained in experiments on the fruits of the rose family, particularly cherries, plums, and apples, and the citrous fruits. In the case of cotton and wheat much effective work is also being done.

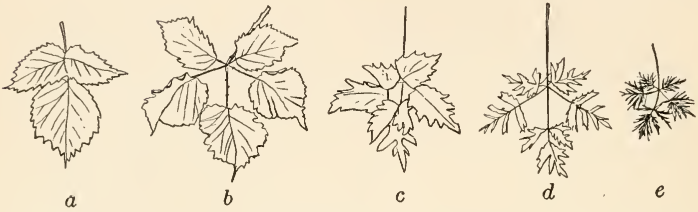

FIG. 379. Five forms of leaf from hybrid blackberries, all grown from the seed of one plant and showing extraordinary variations in the amount of incision in the margins of the leaflets, forming a regular series from *a* to *e*

Modified after Burbank

The extraordinary successes of Luther Burbank in producing new hybrid varieties of fruits and ornamental flowers have been widely discussed in the popular magazines. He has bred some remarkable hybrids, such as those between the strawberry and raspberry, the apple and blackberry, the petunia and the tobacco plant. These are of little use, though of much scientific interest. Others of his hybrids, especially the plums, are of great commercial value. Many other investigators, whose

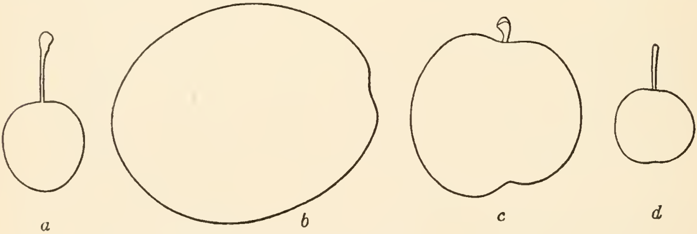

FIG. 380

a, a stoneless wild plum; *b*, *c*, *d*, fruit of hybrids of *a* with the French prune. All drawn to the same scale. — Modified after Burbank results have not received popular notice, are working more directly for useful hybrids, and a few of these may be very briefly summed up.

487. Results of hybridizing citrous fruits. In the plant-breeding laboratory of the United States Department of Agriculture in 1896 and 1897 hybrids were made of the ordinary sweet orange and the uneatable three-leaved orange (*Citrus trifoliata*). Three promising varieties of a new kind of fruit known as citranges have thus been obtained. Two of these are likely to serve as substitutes for lemons, and the third may, to some extent, take the place of grape fruit. Their main value lies in the fact that they can be cultivated from two hundred to four hundred miles farther north than ordinary citrous fruits.

Another interesting hybrid is that between the tangerine and the grape fruit, called the tangelo, which shows a blending of the characteristics of the parent species.

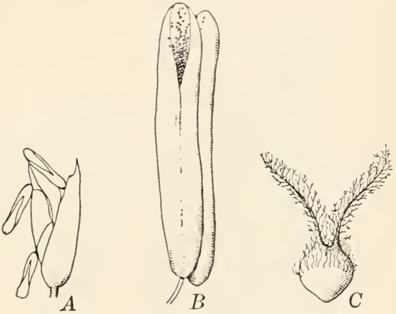

FIG. 381. The flower of the wheat plant

A, entire flower as seen at five in the morning, with the stamens protruding, the pistil remaining inside; *B*, the anther enlarged, showing escaping pollen; *C*, the pistil enlarged, showing the feathery stigmas. — After University of Minnesota Agricultural Experiment Station

488. Results of hybridizing cotton. The cotton produced in the United States is roughly classed as long staple and short staple. The fibers of the former kind are about one and one-half times as long as those of the latter. For many kinds of goods long staple cotton is indispensable, and its price is from one and one-half times to nearly twice as great as the price of short staple cotton. The short staple sorts can be grown over a much larger territory than the others, so that our annual production of long staple cotton is only about one and one-half per cent of our total cotton crop.

Hybrids have been made between the very long-fibered fine sea-island species and the ordinary upland species, and after six generations of selection and careful cultivation some valuable hybrid varieties seem to have been developed.

489. Results of hybridizing wheat. The flowers of wheat are naturally self-pollinated,— that is, the stamens of each flower commonly discharge their pollen upon the feathery stigma of their own flower as soon as the pollen sacs open. This fact makes hybridization much more effective in producing variation in wheat than in plants which are generally cross-pollinated; for in the case of wheat any kind of cross pollination, and especially that between markedly different varieties, may be said to give a sort of shock to the operation of reproduction, and thus produce abundant variation. The details of the process of artificial pollination need not be given. It is successful in a large proportion of cases, and the offspring may be of many types, as shown by Fig. 382. It is found that after the fourth generation an occasional plant may be found which

FIG. 382. Variation in wheat, the hybrid offspring of hybrid parents

After figure redrawn from *Transactions of the Highland and Agricultural Society of Scotland* yields well and will "come true to seed." More important results may be expected in the future from hybridizing wheats than any yet attained.[1]

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[1] The literature of plant breeding is extensive and rapidly increasing. An excellent general account of the subject and full bibliography is contained in *Plant Breeding* by L. H. Bailey, The Macmillan Company, New York and London, 1906.

A valuable summary of the main topics of plant breeding is contained in *Bulletin No. 29*, 1901, of the Division of Vegetable Physiology and Pathology of the United States Department of Agriculture.

Much information is also given in Hugo de Vries, *Species and Varieties: their Origin by Mutation*, Open Court Publishing Company, Chicago, 1905.

Other publications of the United States Department of Agriculture on plant breeding are:

For corn, *Farmer's Bulletin No. 229*, 1905.

For wheat, Bureau of Plant Industry, *Bulletin No. 78*, 1905.

Division of Vegetable Physiology and Pathology, *Bulletin No. 24*, 1900.

The publications of most of the Agricultural Experiment Stations contain much important material for the discussion of plant breeding. A few of these are as follows:

For corn, University of Illinois Agricultural Experiment Station, Circular No. 74, 1904; *Bulletins Nos. 55, 82*, 1902; *87*, 1903; *100*, 1905.

Ohio Agricultural Experiment Station, *Bulletin No. 140*, 1903.

Kansas Agricultural College, *Bulletin No. 107*, 1902.

Nebraska Agricultural Experiment Station, *Bulletin No. 91*, 1905.

For wheat, University of Minnesota Agricultural Experiment Station, *Bulletin No. 62*, 1899.

Ohio Agricultural Experiment Station, *Bulletin No. 165*, 1905.

The authors wish to express their obligations to all the authorities abovementioned. They have also to thank Assistant Secretary Willet M. Hays, of the Department of Agriculture, for his kindness in reading and copiously annotating the present chapter.

CHAPTER XLI

SOME USEFUL PLANTS AND PLANT PRODUCTS

490. Economic botany. The branch of the science which treats of the uses of plants to man is called *economic botany.* Since whole industries like agriculture, lumbering, paper making, and a multitude of others are concerned with the utilization of plants or parts of plants, the subject is a most extensive one and can only be outlined in a general text-book of botany.

A partial classification of useful plant products may be suggested, dividing them into

1. Food products for human use.
2. Medicinal plants and plant products.
3. Food products for domestic animals.
4. Plants used as fertilizers.
5. Plant products used in chemical and other manufactures, as tanning, dyeing, etc.
6. Plant fibers and related products.
7. Timber.
8. Fuel.
9. Ornamental plants.

In general only those members of the classes above given which are of considerable importance in our own country will be mentioned in this chapter.

1. FOOD PRODUCTS FOR HUMAN USE

491. The grains form the most important part of our vegetable food; they are the fruits of the *cereals,* or food-producing grasses, and for this and other reasons the grasses, which in all number about 3500 species, are more useful to man than any other family of plants. The principal genera of cereals are wheat, oats, rye, barley, rice, and Indian corn. Most of the cereals are grass-like herbs of moderate height, but corn varies much in size, from some of the dwarf varieties of pop corn not more than two feet high to the twenty-foot field corn of the rich river bottoms of the Middle West. All the grains have many varieties, but these are most familiar in the various sorts of wheat — hard, soft, red, white, bearded, beardless, and so on — and in the many qualities of grain of Indian corn (see Chapter XL).

Wheat is the most important of the cereals, on account of its palatableness, high food value, and ready digestibility. None of the other grains yield a flour which is as well adapted for bread making as wheat flour. Rice is readily digestible, but is inferior to most grains in the relative proportion of proteids to other ingredients; and oats, rye, barley, and Indian corn, as usually prepared, are somewhat difficult of digestion. Corn meal when imperfectly cooked, and eaten to the exclusion of other food, has often given rise in northern Italy to a much-dreaded disease known as *pellagra*.

Fig. 383. A cornfield in Missouri

After Frye

The United States is the leading wheat- and corn-raising country, producing more than one fourth of the total world's crop of the former grain and four fifths of the latter.

Any of the grains may be made to yield starch for food or for laundry or manufacturing purposes, but the greater part of that produced in this country is obtained from corn, which contains about 60 per cent of it. Moldy or otherwise damaged grain can be utilized to some extent in starch making.

Corn also contains in the embryo of the grain from 3 to 6 or more per cent of oil, which is now largely extracted for use as food and for various manufacturing purposes.

492. Leguminous seeds. Several kinds of seeds of the pea family (*Leguminosæ*) — an immense family, comprising some 7000 species — are important articles of food. Beans, as every one knows, are used as food in all stages, from the time when the pods are half grown until the seeds are entirely ripe and dry. In the latter condition, when properly cooked, they constitute one of the cheapest and most concentrated forms of proteid food.

Peas, whether "green" or dry, have much the same nutritive value as beans in the same stage of maturity. Various canned products of beans and of peas are now prepared on a large scale.

Peanuts are the seeds of a leguminous plant which forces its growing pods underground, where they remain during and after the process of ripening. The domestic consumption of these seeds is large, and they constitute a considerable article of export.

Several other kinds of leguminous seeds, such as broad beans, lentils, and chick peas, are extensively used as foods in parts of Europe, but are not as yet important articles of diet in our own country.

493. Other seeds. The remaining kinds of seeds which are important as food are mostly known as nuts. Some of these are really drupes, like the cocoanut and the walnut (Sec. 183, Fig. 166, V), while others, like the Brazil nut and chestnuts, are seeds.

From the palm family, which is of supreme importance within the tropics, only one kind of so-called nut, the cocoanut, is commonly in use among us. The abundant endosperm of its seed is largely eaten raw and much used in cookery.

Three rather closely related families of trees — the walnuts, the birches, and the beeches — furnish most of our edible nuts. From the first come walnuts, butternuts, pecans, and hickory nuts; from the second, hazelnuts and filberts; and from the third, beechnuts and chestnuts.

The rose family furnishes almonds, which are technically drupes, closely related to peaches (Fig. 164).

Brazil nuts are the seeds of lofty South American trees of a tropical family allied to the mangroves and the myrtles.

Fig. 384. A grove of cocoa palms in the Philippines
After Frye

494. Chocolate, tea, and coffee. These familiar substances are derived from plants of three different families, the first two being somewhat nearly related tropical or sub-tropical ones.

Chocolate consists of the ground or crushed seeds of the cacao tree, a native of Mexico, now widely cultivated throughout the tropics. Removal of a large part of the aromatic fat known as cacao butter, which is considerably used in medicine, leaves cocoa, which forms for some people a more digestible beverage than chocolate.

Tea is made from the leaves of a shrub long cultivated in China and Japan, and now also in India, Ceylon, and elsewhere. Unlike chocolate, tea has no food value, but is a mild stimulant.

Coffee is made from the seeds of a small tree widely cultivated in hot countries and belonging to the madder family. The seeds are produced in red berries, which are thickly clustered about the twigs of the tree. Coffee has only a trifling food value, but is a vigorous stimulant, reënforcing the action of the heart.

Fig. 385. A flowering twig of the coffee tree

Two thirds natural size, with fruit *f* and *fs* and seeds *s*, natural size. — After Wossidlo

495. Fruits with fleshy pulp. The kinds of fruit with fleshy pulp, some eaten raw and others requiring cooking, are so numerous that they can only be mentioned under the families to which they belong.

From the palms are obtained dates, which are technically berries with a very hard seed. In the arid portions of Africa and northwestern Asia, where they grow, they are of the first importance as food. Successful attempts are now in progress to introduce the culture of the date palm into the desert regions of the extreme southwestern United States.

Plate XIII. A tropical forest in the Philippines, mainly palms

After F. W. Atkinson

From the pineapple family our only edible fruit is the pineapple, largely cultivated in Florida and the West Indies.

The banana family is a very small one, but exceedingly important, since it furnishes, in the shape of bananas, the principal subsistence of multitudes of the inhabitants of the tropics. The plant is herbaceous, but sometimes grows to the height of forty feet, with enormous leaves. It is extraordinarily productive, so that a few square rods of good soil set with banana plants will supply the fruit for an entire family. Our importation of bananas is very large and rapidly increasing, and what was once an article of luxury or a curiosity is now the staple fruit for the entire year in most of our markets. The principal supply comes from the West Indies and Central America, but bananas are somewhat cultivated in the extreme southern portions of the United States.

The mulberry family supplies the breadfruit, which constitutes the most important food of great numbers of the inhabitants of the south Pacific Islands. Our only fruits of this family are the mulberry and the fig. Most of our figs are still imported, but their culture has recently become a considerable industry in California, since the variety which can be dried for shipment is now successfully cultivated there.

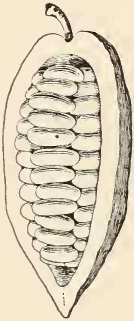

Fig. 386. A cacao pod, cut open to show the seeds

One fourth natural size. — After Schmidt

Two closely related groups, the saxifrage family and the rose family, furnish a large proportion of all our true berries, and some edible fruits which are not berries. From the former family are obtained currants and gooseberries. The rose family consists of five sub-families. Of these the apple subdivision furnishes quinces, pears, and apples; the rose subdivision furnishes strawberries, blackberries, and raspberries; and the plum subdivision furnishes plums, cherries, peaches, apricots, and nectarines.

The rue family contains a rather small number of trees and shrubs, with only two common genera, the prickly ash and the hop tree in temperate North America, and comprises, among others, the orange sub-family. Under this is found the genus *Citrus*, which embraces all the citrous fruits. The species and varieties which are found in our markets may be classed as oranges, grape fruit, and lemons.

Most of our oranges are now of American growth, coming from California or Florida, and many of the very large fruited species of *Citrus* from Polynesia, variously known as pomelo and grape fruit, are raised in both these states, while some are also imported from the West Indies. The best lemons are imported from the Mediterranean coast, largely from Sicily.

The grape family numbers about 300 species of climbing shrubs. Only the grape genus *Vitis* is a source of edible fruits, — the berries so familiar as fresh grapes or raisins.

Of these there are two principal types, one comprising the European (Malaga and other) varieties with solid pulp, found also in such California varieties as the Tokay grape, all of which are descended from one European species. The other type is the one with soft pulp, readily separated from the skin, such as the Catawba, Delaware, Isabella, and Concord varieties. These have to some extent been introduced into Europe, but are descendants of native American species. Grapes are considerably cultivated in most of the states, but nowhere else so extensively as in California, where they are raised for wine making, for the manufacture of raisins, and for shipment in a fresh condition.

The heath family supplies berries of several species, such as the familiar cranberries and the blueberries and huckleberries, which are largely gathered for the market in several of the northeastern states, particularly in Maine, and are somewhat extensively canned.

From the olive family (mostly sub-tropical trees and shrubs) are obtained olives, which constitute a table delicacy, while the oil is a highly valuable food.

From the nightshade family, many of which are poisonous plants, we get several large edible fruits (true berries, though they are not popularly so called), — the ground cherry, or strawberry tomato (*Physalis*), the pepper (*Capsicum*),[1] the egg plant, and the tomato.

The gourd family furnishes all the melons, cucumbers, squashes, and pumpkins.

496. Edible leaves and shoots. Only a few of the articles of diet under this head have much commercial importance or form a notable part of the subsistence of people in any portion of the country.

From the lily family we get asparagus; from the pigweed family, spinach; from the mustard family, water cress, cabbage, cauliflower, and Brussels sprouts; from the parsley family, celery; and from the *Compositæ*, lettuce and globe artichokes (*Cynara*).

497. Edible bulbs, rootstocks, tubers, and roots. As is elsewhere explained (Sec. 66), reserve material is often stored in underground portions of the plant body. The number of vegetables derived from these is not very large, but they constitute a considerable part of the food of people, especially in temperate and cold climates.

From the lily family onions are obtained, from the yam family yams, from the pigweed family beets, from the mustard family turnips and radishes, from the parsley family carrots and parsnips, from the morning-glory family sweet potatoes, from the nightshade family potatoes, and from the *Compositæ* salsify and Jerusalem artichokes (*Helianthus*).

498. Starch and sugar from stems and roots. Sago is the purified starchy pith of small palms, natives of Siam and of some of the Malayan Islands. A portion of the supply also comes from West Indian cycads (Sec. 346).

Tapioca is a starchy substance obtained from the grated roots of plants of the spurge family (*Euphorbiaceæ*), cultivated in tropical America and the West Indies.

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[1] This is not a pulpy fruit.

Arrowroot is a very pure starchy food obtained from the rootstocks of plants of two or three tropical families, especially the arrowroot family (*Marantaceæ*).

FIG. 387. Sugar cane (*Saccharum*)

Much reduced. — After Wossidlo

Sugar is largely manufactured in Europe and to some extent in the United States from the juice of the sugar beet. The remainder of the world's supply of sugar comes from the stem of the sugar cane, a grass which grows to a height of ten feet or more. It is somewhat cultivated in Louisiana, but much more extensively in the West Indies, Java, and the Hawaiian Islands.

2. MEDICINAL PLANTS AND PLANT PRODUCTS

499. The study of medicinal plants is a special subject, forming an important part of the course in every college of pharmacy. Only a few words can be given to the topic in this chapter.

Very many of the families of angiosperms contain species used in medicine.[1] In some cases, as in the lily family, the pea family (which furnishes sixteen remedies), the mint family,

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[1] In the United States Pharmacopœia sixty-seven families are represented.

and the nightshade family, medical properties are quite generally distributed throughout the whole family or through certain sections of it. In other cases, as in the poppy family (which yields opium and morphia), the family *Erythroxylaceæ* (which yields cocaine), and the figwort family (which yields digitalis), only one important remedy or group of remedies occurs. The properties of many medicinal plants were discovered by accident in primitive times, while others have had their value established only as a result of careful experiments on man and the lower animals.

3. FOOD PRODUCTS FOR DOMESTIC ANIMALS

500. The most important herbivorous domestic animals — cattle, horses, and sheep — consume large quantities of the less expensive grains, and in general the roots and tubers which are useful for human food are readily eaten by these animals.

A large proportion of the grasses are utilized by grazing animals or fed as hay. Many plants of the pea family, particularly alfalfa, the clovers, soy beans, and cow peas, are eaten by domestic animals.

Both grasses and other plants are cut and fed to cattle and horses, while fresh, as *forage*. Large quantities of "corn fodder" are used in this way in many parts of the country, and the stems and leaves of corn are also cut up, placed in large tanks called *silos*, allowed to ferment, and then fed to cattle throughout the winter.

Certain by-products of manufacturing processes are of much value for cattle food. Among the most important of these are linseed meal and cotton-seed meal, which are rich in proteids and still retain some oil after the greater part of it has been extracted by the most powerful pressure available. The refuse grains from breweries and the sloppy boiled corn meal from distilleries are in a wet state extensively fed to cattle and hogs, but are injurious if used alone. They are also dried for shipment. The refuse from beet sugar manufacturing establishments is used in a wet condition for cattle feeding, and is also dried and shipped.

Some seeds not eaten by man are highly valuable when fed to the lower animals. Acorns and beechnuts, for example, in some of the wooded portions of the southern Middle States, furnish a considerable part of the subsistence of droves of hogs.

4. PLANTS USED AS FERTILIZERS

501. For centuries the advantage of plowing under growing crops as a means of enriching worn-out land has been well recognized. It is only very recently that the exact significance of this process has been understood. Even now the details are not so fully worked out that we know just what crop will yield the best results for every variety of soil and climate; but in a general way it is established that leguminous plants are the best for this purpose on account of the power which their root tubercles have of utilizing the nitrogen of the atmosphere (Sec. 256). Various clovers and alfalfa are the crops most commonly employed.

5. PLANT PRODUCTS USED IN MANUFACTURES

502. Under this head there is only space to mention a very few of the vegetable substances used in manufacturing processes, most of them on account of their chemical properties.

Dyeing by means of vegetable coloring matters is far less important than it was before the introduction of the artificially prepared aniline colors. These are so powerful that it is more economical to use them, but they do not give soft shades. Valuable dyes, however, are still obtained from a considerable number of plants. Many of these belong to members of the pea family, which furnishes Brazil wood (red), logwood (red, purple, and black), camwood (red), indigo (dark blue).

From the buckthorn family are obtained yellow and green dyestuffs, known, respectively, as Persian berries and Chinese green indigo.

Varnishes of great value are yielded by trees of the pea family (copal varnish) and of the sumach family (Japanese lacquer).

Tanning is largely carried on by aid of the bark of several species of oak, of which the black oak and the Spanish oak are two of the most used American species. Hemlock bark and the leaves and young twigs of Sicilian and American species of sumach are also used for tanning. Other substances employed for the same purpose are catechu, derived from a species of acacia, and gambier, derived from the evaporated sap of a tree of the madder family, a native of the East Indies.

Fig. 388. A twig of the South American rubber tree (*Hevea*)

After Schmidt

India rubber is manfactured from the sap of several tropical trees and lianas. The principal one of these is the Para rubber tree (*Hevea*) of the spurge family.

Gutta-percha is produced by trees of the star apple family (*Sapotaceæ*) of the Malay Archipelago, a family of much economic importance.

6. PLANT FIBERS AND RELATED PRODUCTS

503. Fibrous materials for use in spinning into thread, cordage, and rope, also for braiding and weaving, are obtained from many parts of the plant body. Some of the most useful of these, such as flax and hemp, are derived from the hard bast, others, as cotton, consist of plant hairs, and others still represent various structural elements of the plant.

A large proportion of the fibrous materials in general use comes from monocotyledonous plants of several families.

Fig. 389. A Georgia cotton field

After Frye

Several sedges of the genus *Cyperus* furnish materials for weaving, and East Indian and Chinese mattings are made from species cultivated for the purpose.

The straw of various grains is employed for braiding into baskets, mats, hats, and other articles. A coarse grass known as *esparto* is largely exported from Spain and the North African coast for use in paper making and for other purposes.

Many palms produce valuable fiber; that of the husk of the cocoanut is largely used for cordage, mats, brushes, and similar articles.

From material obtained from the very young leaves of a somewhat palm-like plant (*Carludovica*) the well-known Panama hats are woven.

Several plants of the lily family, especially the so-called New Zealand flax and the century plant (Fig. 391), furnish fibers.

Fig. 390

A portion of a cotton plant in bloom with a ripe capsule or boll *b* and seed *s*. All slightly reduced. — After Wossidlo

From a member of the banana family, a native of the Philippines, but cultivated also in India, is obtained the extremely valuable manila fiber, one grade of which is so fine as to be woven into delicate shawls and similar fabrics, while the coarser kinds are used in the manufacture of manila rope.

Among dicotyledonous plants there are a considerable number which serve as sources of commercial fibers.

To the mulberry family belong the paper mulberries, which furnish bark from which the beautiful Japanese paper is made, and the hemp plant, which is one of the chief rope- and cordage-making materials.

To the nettle family belongs ramie, an eastern Asiatic plant cultivated in Jamaica and the southern United States, from which Chinese grass cloth and other fabrics are made.

Three closely related groups of plants — the linden family, the mallow family, and the silk cotton family — yield many fibrous or hair-like products of use for spinning and weaving, or for mattress making and similar purposes. From the bark of trees of the first-named family is obtained the Russian bass, or bast, used for making rough mats, and the tropical product jute, used to weave with silk, and also for carpets, mats, and coarse bags. From the hairs which clothe the seed of the cotton plant (the most important member of the mallow family) all cotton goods are manufactured. Cotton is largely cultivated in India, Egypt, and our own country. It is an important crop in all of our Gulf states, and in Georgia and South Carolina. The seed hairs of the tropical silk cotton trees (*Ceiba*) are coming to be much used in pillows and cushions as a substitute for feathers.

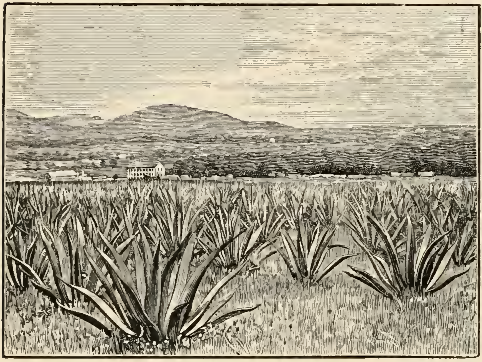

Fig. 391. Century plants (*Agave*)

After Frye

Most vegetable fibers, such as have been described in this chapter, are useful for paper making, even after the rope or woven fabrics made from them have been worn until they are dropping to pieces. Large areas of forest, particularly of spruce and poplar growth, are now annually cut down to furnish paper pulp. It has been recently proposed to utilize cotton stems for paper pulp. Ten million or more tons of the raw material, worth nearly a dollar a ton for this purpose, are now annually available in the cotton-growing states.

7. TIMBER

504. Coniferous woods. The wood of our cone-bearing trees (mainly of the pine family) is generally known as soft wood, and that of our broad-leaved, mostly deciduous trees is known as hard wood. These terms are not quite correct, for the coniferous larches and yews furnish a harder wood than that of such broad-leaved trees as willows, poplars, tulip trees, and buckeyes.

Fig. 392. Forest of hard or yellow pine (*Pinus palustris*) on southern coastal plain of the United States

After Frye

Out of the entire timber supply of the country more than three quarters is at present furnished by the thirty-eight or more species of cone-bearing trees, especially the pines, which grow within our limits.

The wood of the white pine (*Pinus strobus*), remarkable for its workableness and freedom from warping or cracking when exposed to the weather, was for years the most important of all our soft woods. Latterly, as the supply is becoming greatly lessened, other kinds of pine, especially the long-leaf pine, the loblolly pine of the southeastern states, and the bull pine (*P. ponderosa*) of the Pacific and Rocky Mountain regions, are to a considerable extent taking its place.

Among the other most widely used coniferous woods are two species of true spruce (*Picea*), the "Douglas spruce" (*Pseudotsuga*), two western species of white fir (*Abies*), the smaller California redwood (*Sequoia*), the American or bald cypress (*Taxodium*), and several distinct kinds of white cedar (*Thuya*, *Chamæcyparis*, and *Libocedrus*). The cypress, larch, and most of the cedars furnish timber of great durability when exposed to the weather or buried in the earth, and therefore are highly valued for posts, telegraph poles, railroad ties, and similar uses.

505. Broad-leaved woods. Our native broad-leaved trees which furnish wood for manufacturing or constructive purposes comprise about eighty species, a larger number than is found in any other equal area of the temperate zones.

The principal hard-wood forests are of oak, though other valuable timber trees, such as maples, hickories, beeches, and elms, are usually scattered among them. Our oak lumber is of three kinds, — white, red, and live oak. White oak is much superior to red for constructive purposes where strength is important, but does not show so conspicuous a grain when polished for cabinet work. More than half of our supply of hard woods comes from various species of oak.

Next in importance is the wood of the tulip tree (*Liriodendron*), generally known as yellow poplar, or whitewood. This has largely taken the place of white pine in inside woodwork for dwelling houses and other buildings.

Among the most generally useful of the other broad-leaved woods may be mentioned maple, elm, ash, and chestnut.

Several kinds are particularly valued for their durability in the ground; among these are chestnut, black locust, and catalpa.

For cabinet work the most prized of our native woods are black walnut, cherry, birch, and some species of oak. None of these is as beautiful as some of the finer imported kinds, such as mahogany, rosewood, and satinwood.

Fig. 393. Hickory (hard wood) forest near southern end of Appalachian highlands

After Frye

506. Forestry. During the time when the country was in process of being settled most portions of the Atlantic coast region, and inland as far as the prairies of what are now the states of Illinois and Minnesota, were covered with primitive forest. The most difficult task of the settler was to clear enough land for tillage. The finest timber trees were destroyed by hundreds of thousands by the process of girdling, that is, by cutting away a ring of sapwood and allowing the trees to die of starvation and lack of water. Cultivation was carried on among them, until after some years the trees would fall and then were burned to rid the land entirely of their presence. More than a century and a half of wholesale destruction of trees has finally resulted in stripping large areas of the original forest and preventing the reforestation of the land, until

Fig. 394. A corn field in a "deadening" or girdled forest of deciduous trees

Modified after Ayres

a point has been reached when it is difficult to get lumber of good quality for many of the most important purposes for which it is used. In some parts of the country timber is a profitable crop to raise, even if it has to be planted and cared for while growing. The science and art of growing timber and caring for tracts of wooded land is called *forestry*. Much attention has long been paid to it in the most enlightened countries of Europe, but the subject is a comparatively new one in the United States. The importance of maintaining a suitable proportion of wooded land in any region does not depend merely on the desirability of a supply of timber. The water supply of lakes and streams, the retention of the cultivable layer of loam on the earth's surface, the climate of any region, at least so far as the prevention of severe winds is concerned, — all are dependent on the presence of considerable forest areas.

The principles of forestry cannot be laid down in a few words, and forest management requires years of study in the woods themselves. The literature on the subject is extensive, and courses in forestry are now given in a good many universities. Evidently it is a topic of growing importance in this country. A few useful rules can be given here.

1. Tree cutting should generally be managed on the principle of selecting only mature trees and leaving the others to grow up to replace those cut.
2. Forest fires should be prevented.
3. Destructive fungi should be exterminated wherever found.
4. Insect enemies of trees, such as the seventeen-year locust, the various caterpillars, and boring insects, should be destroyed.
5. Sheep and cattle should never be pastured in woods where they can do harm by killing young seedling trees or other useful undergrowth.
6. Tree planting should be carried on whenever it can be made to utilize lands not needed for other purposes, and the species planted should be chosen with extreme care to meet the requirements of the soil and climate.

8. FUEL

507. Nearly all fuel is of vegetable origin. In most civilized countries to-day the principal fuel supply consists of various kinds of coal, that is, of vegetable matter which has been buried in the earth for ages and undergone many changes (Sec. 330).

Peat, the consolidated material left after the partial decay of certain bog mosses (Sec. 292), in some countries forms a considerable part of the available fuel, and the deposits in the northern United States are of some importance.

Wood, in portions of the country, is still the principal fuel. Certain varieties are preferred for household use on account of their furnishing good beds of glowing coals, or for burning in open fires on account of their freedom from any tendency to snap. But in general the fuel value of thoroughly seasoned wood is nearly proportional to its weight per cubic foot, that is to say, the very heaviest woods, such as hickory, the white oaks, black locust, and some kinds of ash, are worth most for heating.

Other parts of plants besides wood are used to some extent for fuel. In large tanneries the spent bark is often compressed to extract most of the water and then burned. Corncobs are often burned in stoves and under steam boilers. In treeless regions twisted ropes of straw are used as fuel.

9. ORNAMENTAL PLANTS

508. Our ornamental plants may be roughly classed into shade trees, shrubs, herbaceous perennials, and annuals. The total number of species and varieties cultivated in the United States runs far into the thousands, but in many cases florists' varieties are distinguished from one another only by color or some other comparatively unimportant characteristic.

Most of our cultivated ornamental plants are of foreign origin, and representatives of almost all parts of the earth except the arctic regions are found among them. In a few instances native species are familiar occupants of our flower gardens, as, for example, the native azaleas and *Rhododendrons*, the bee balm, California poppy, evening primrose, Mariposa lily, Missouri currant, purple flowering raspberry (*Rubus odoratus*), cone flower (*Rudbeckia*), snow on the mountains (*Euphorbia*), and wild cucumber.

Some of the families which contribute most largely to our lists of cultivated flowers are the lily, the amaryllis, the pink, the crowfoot, the rose, the pea, the geranium, the heath, the mint, and also the composite family.

APPENDIX

[*Additional illustrations, chiefly for use with a flora in determination of species*]

I. LEAF FORMS

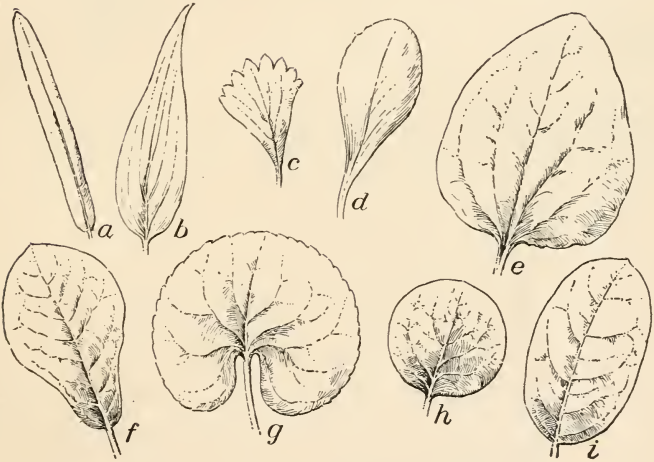

FIG. 1. General outline of leaves

a, linear; *b*, lanceolate; *c*, wedge-shaped; *d*, spatulate; *e*, ovate; *f*, obovate; *g*, kidney-shaped; *h*, orbicular; *i*, elliptical

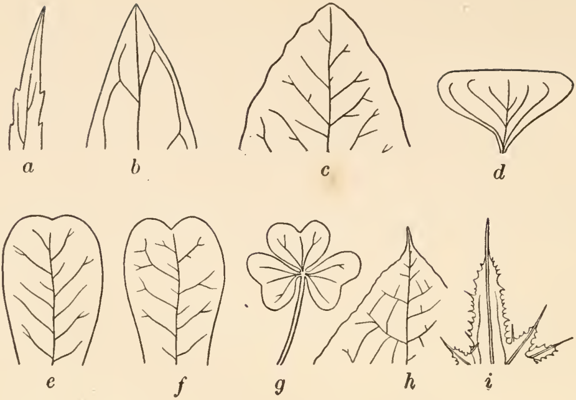

Fig. 2. Tips of leaves

a, acuminate or taper-pointed; *b*, acute; *c*, obtuse; *d*, truncate; *e*, retuse; *f*, emarginate or notched; *g* (end leaflet), obcordate; *h*, cuspidate, — the point sharp and rigid; *i*, mucronate, — the point merely a prolongation of the midrib

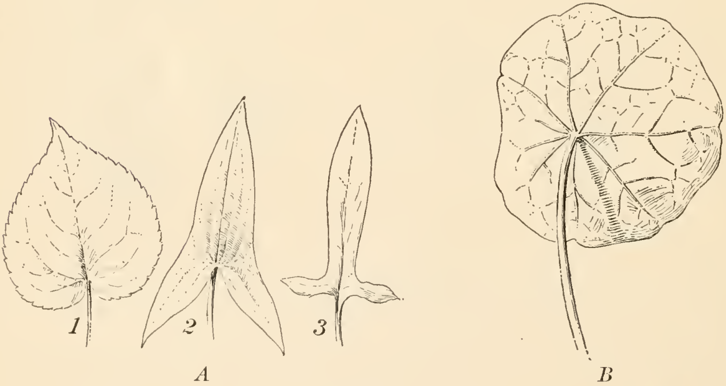

Fig. 3

A, shapes of bases of leaves: 1, heart-shaped; 2, arrow-shaped; 3, halberd-shaped. *B*, peltate leaf of tropæolum

II. FORMS OF SYMPETALOUS COROLLA

FIG. 4

Bell-shaped corolla of bell-flower (*Campanula*)

FIG. 5

Salver-shaped corolla of jasmine (magnified)

FIG. 6

Wheel-shaped corolla of potato

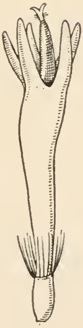

FIG. 7

Tubular corolla, from head of bachelor's button

FIG. 8

Labiate or ringent corolla of dead nettle

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References to illustrations are indicated by stars. App. indicates Appendix

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